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FACTORS INFLUENCING THE JUVENILE DEMOGRAPHY OF A CORAL REEF FISH

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Abstract. A notable recent development in marine ecology has been the suggestion that the size of demersal populations is limited and that patterns in demersal abundance are determined by the settlement of pelagic larvae (recruitment). Here I examine some factors potentially limiting and determining population density in a small coral reef fish. An experimental study of the demography of juveniles of a small planktivorous damselfish, the humbug *Dascyllus aruanus* (Pomacentridae), was done at One Tree Reef, southern Great Barrier Reef, Australia. Recently settled fish were transplanted to replicate units of habitat at three lagoonal sites. The interactive effects of initial recruit density, the presence of adults, and supplemental feeding on the growth, survival, migration, and maturation of the recruits were examined over the following 10 mo.

Migration was apparently rare and thus unimportant. Effects of the factors on the growth and survival of recruits were complex. Survival of recruits was generally inversely related to their density but enhanced in the presence of adults. Average survival also varied among locations. Mean growth was generally depressed at high recruit densities and in the presence of adults but was enhanced by supplemental feeding. Maturation was related to size and so was influenced by effects on growth. The results suggest that regulatory interactions and shortages of food may limit the size of adult populations via their effect on growth rates. Effects of the factors on survival were slight. Total abundance may thus be limited primarily by recruitment unless effects on growth are ultimately translated to effects on demersal mortality.

As a result of the effects on survival, there was some modification of the initial pattern of recruit abundance. The importance of these effects in determining patterns of abundance in unmanipulated populations depends on variation in recruitment at similar scales. The number of recruits entering the adult population under different treatments was highly modified from the pattern of initial recruit density. The number of recruits that became mature by the end of the experiment was totally unrelated to their initial density. In addition, that number was reduced in the presence of adults, and was limited by the availability of food.

The results suggest that complex effects of these factors on juvenile demography can modify recruitment patterns at small spatial scales. They also suggest that these factors may have different effects on the adult and total demersal populations. In general terms, both recruitment and postrecruitment processes influence patterns in abundance.

Key words: coral reefs; *Dascyllus aruanus*; density dependence; food limitation; growth; maturation; mortality; Pomacentridae; population dynamics; recruitment.

INTRODUCTION

Many marine organisms, including fishes, have larvae that undergo a pelagic dispersive phase before settling to their adult habitat. Recruitment to demersal populations occurs by the settlement of larvae, or already metamorphosed individuals (Kingsford 1988). Because of difficulties with measuring settlement, recruitment is often operationally defined as the first sighting in the adult habitat of a settled juvenile (Richards and Lindeman 1987). It may then include the effects of early postsettlement events (Keough and Downes 1982). The extent of variation in settlement/

recruitment and its implications for the abundance and diversity of marine organisms has received much attention in recent years (Underwood and Denley 1984, Connell 1985, Lewin 1986, Doherty and Williams 1988, Mapstone and Fowler 1988, Underwood and Fairweather 1989). Variation in recruitment is an important component of recent models of the organization of marine communities (Menge and Sutherland 1987, Roughgarden et al. 1987) including fish communities on coral reefs (Sale 1977, Talbot et al. 1978, Chesson and Warner 1981).

Severe mortality of larvae, coupled with their presumed widespread dispersal means that the magnitude of settlement to an area of demersal habitat should be uncorrelated to the fecundity of the resident breeding population (Scheltema 1971). Local demersal populations may thus be viewed as open systems. The pro-

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cesses responsible for the dynamics of demersal populations are, therefore, settlement and demersal mortality though, for mobile organisms such as fishes, postsettlement dispersal must also be considered.

Two models have been developed that propose a major role for settlement in the population biology of marine organisms. The first model pertains to the limitation of population density. By definition, a factor is limiting if population density increases or decreases as the factor increases or decreases. A common assumption of studies on marine invertebrates (e.g., Connell 1961, Dayton 1971) and early models of species coexistence for coral reef fishes, namely the niche diversification model (Smith and Tyler 1972) and the lottery competition model (Sale 1978), was that demersal populations were oversupplied with potential recruits. Competition (*sensu* Andrewartha and Birch 1954) for space, which resulted in density-dependent recruitment and/or survival was hypothesized to limit the density of individual species of fish (under the niche diversification model) or the combined density of guilds of competing species (under the lottery model). In the early 1980s Doherty (1981, 1982, 1983) and Victor (1983) presented evidence suggesting that the density of populations of reef fishes was limited by recruitment, more precisely the supply of larvae, rather than competition. This model was termed the recruitment limitation model (Doherty 1981).

The second model refers to the determination, or control (*sensu* Varley et al. 1973), of spatial and temporal variation in population density. For demersal populations this will depend on the strength and relative variability of the factors affecting settlement and postrecruitment demography. Fluctuations in settlement from the plankton have been implicated in controlling the abundance of a range of marine species (Coe 1953, Yoshioka 1982, Connell 1985). Doherty (1981) and Victor (1983) proposed that settlement to populations of coral reef fishes is a function of the supply of larvae and that settlement variation is the major cause of variation in population density. This implies that patterns in the abundance of cohorts generated at settlement are not modified by subsequent processes. This second model has been confused with the recruitment determination model in the reef fish literature (Jones 1987a, Doherty and Williams 1988, Mapstone and Fowler 1988) and so for clarity I will refer to it as the recruitment determination model.

Here I present the results of an experimental study that examined the simultaneous influence of two aspects of local density and the availability of food on the juvenile demography of a small coral reef fish. I evaluated the role of these factors in limiting and determining benthic density. The basic approach was to artificially create a pattern of recruitment by transplanting recently settled fish to replicate units of habitat at three local sites and to then follow the fates of the recruits over the subsequent 10 mo. The study species,

the humbug (*Dascyllus aruanus* L.), a small planktivorous damselfish occurs naturally on small isolated colonies of certain branching corals and so is a good subject for experimental manipulations of this sort (e.g., Sweatman 1985a, b, Jones 1987b).

Since the proposal of the niche diversification and lottery models, a number of studies have tested for limitation of reef fish populations by space resources. Most of these studies have not detected it (Robertson and Sheldon 1979, Robertson et al. 1981, Warner 1984 [cited in Doherty and Williams 1988], two exceptions are Shulman 1984 and Hixon and Beets 1989). The possibility that populations might be limited by the availability of food has received less attention. There have been some suggestions based on circumstantial evidence that food may be limiting for some species (Hobson and Chess 1978, Thresher 1983). Jones (1986) found that short-term growth of another planktivorous damselfish (*Pomacentrus amboinensis*) was significantly enhanced by supplemental feeding, but there have been no tests of the effects of food limitation on population size. Interactions within groups of humbugs suggest a strong potential for competition for food amongst group members. Behaviorally dominant larger fishes tend to feed farther upstream from the home coral than smaller ones and thereby restrict the access of smaller fishes to preferred prey items (Coates 1980a, G. E. Forrester, *unpublished manuscript*). For this combination of reasons, I tested the hypothesis that the availability of food did not affect the demography of juvenile humbugs by supplemental feeding.

Following the initial association of density dependence with competition (Doherty 1981), a few researchers have tested for regulatory interactions amongst coral reef fishes. These studies have produced differing results (Doherty 1982, 1983, Jones 1987a, b, 1989). I manipulated both the density of recruits and the presence of adults at the scale of individual corals (i.e., the scale at which individuals interact). This allowed me to test for regulatory interactions both among recruits and between adults and recruits. Interactions between adults and recruits are of particular interest for humbugs for two reasons: firstly because they live in social groups containing individuals of all sizes, within which there are strong dominance relations based on size (Coates 1980a, G. E. Forrester, *personal observation*), and secondly because larvae have been shown to settle preferentially to corals occupied by conspecific adults (Sweatman 1985b).

There has been much study of patterns and variability in recruitment since the proposal of the recruitment determination hypothesis. Recruitment has been shown to vary considerably on a number of spatial and temporal scales for all tropical reef fishes studied to date (reviewed by Doherty and Williams 1988). In contrast, studies of variability in postrecruitment demography are few. The limited evidence available suggests that there is often considerable intraspecific variability

in natural mortality rates, both interannual (Aldenhoven 1986, Eckert 1987, Mapstone 1988) and at small spatial scales (Aldenhoven 1986, Victor 1986, Mapstone 1988, Robertson 1988). While the abundance of some species may be determined by recruitment (Victor 1983, 1986) the studies of postrecruitment processes indicate that they have the potential to modify recruitment patterns (Aldenhoven 1986, Eckert 1987, Shulman and Ogden 1987) and have in some cases been shown to do so (Robertson 1988, Hixon and Beets 1989).

This experiment was replicated at three local sites. By examining the degree to which the pattern of recruitment I created was modified by subsequent processes, I could examine the degree to which the abundance of the cohort was recruitment determined both at the scale of individual corals and sites within a reef.

METHODS

Study site

This study was done at One Tree Reef (23°30'S, 152°06'E), southern Great Barrier Reef. One Tree Reef is a platform reef (Maxwell 1968) enclosing a protected lagoon system (see Davies et al. 1976 for a more detailed description of One Tree Reef). This experiment was done at three sites in the south eastern corner of the largest lagoon (Fig. 1). Each site was a broad expanse of sand, 2–3 m deep at low tide, with few natural patch reefs. Site 1 was bordered on one side and site 2 on three sides by continuous emergent reef. The only large reef area close to site 3 was a large patch reef ≈ 50 m from its edge. Site 2 may experience generally lower flow rates than the other two sites (Ludington 1979).

Construction of standard coral units (SCUs)

In order to reduce possible variation in demographic processes due to variability in habitat characteristics (Jones 1989), the experiments were done using "standard coral units" (SCUs; after Sweatman [1983]). These structures provide similar replicate units of habitat of a kind that is close to the fishes' natural one. Structures of a similar nature have been used successfully in previous studies by Sweatman (1985a, b) and Jones (1987b).

The construction of SCUs is shown in Fig. 2. A steel fencing post was driven into the sand, then 2–3 pieces of live *Pocillopora damicornis* were tied around the stake with wire and/or fishing line to form a roughly spherical colony of volume ≈ 0.034 m³. This is slightly larger than the mean volume of occupied *P. damicornis* colonies at One Tree Reef (G. E. Forrester, *personal observation*). The colony was suspended ≈ 0.2 m above the sand surface, as coral placed on the sand dies quickly. SCUs ($n = 24$) were built in a haphazard array on each of the three experimental sites during December 1986. Each SCU was situated 20–25 m from any other experimental or natural reef.

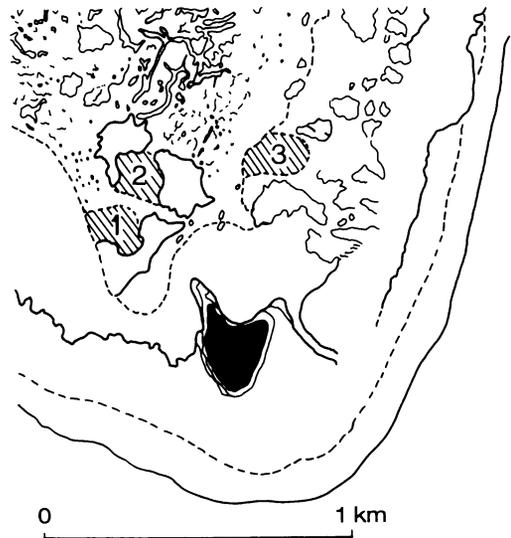


FIG. 1. A map of the southeastern corner of One Tree Reef showing the experimental sites (hatched areas numbered 1–3) and their proximity to One Tree Island (solid black).

Design

A factorial design with four factors was used for this experiment (Table 1). The levels of recruit density were chosen to reflect the range of natural recruitment levels to *P. damicornis* at One Tree Reef (Table 2). The density of adults used for the adults-present treatment is close to the mean density on occupied *P. damicornis* corals at One Tree Reef (4.4 adults/0.034 m³, G. E. Forrester, *personal observation*). There are also many unoccupied corals, so the adults-absent treatment is also relevant to the natural situation.

Preparation of SCUs

Four adults were introduced to each of the adults-present SCUs between 12 and 15 December 1986. Introduced fish were collected from social groups occupying colonies of *P. damicornis* in another part of One Tree Lagoon. Fish were collected by chasing them into their home coral, surrounding the coral with a net, anaesthetizing the fish under the net using the anaesthetic quinaldine and then capturing the required fish using hand nets. The adults placed on any one SCU were all captured from the same group because transplanting groups of adults with established dominance hierarchies greatly reduces aggression and emigration of transplanted fish. All fish introduced were >40 mm FL (FL = fork length, which is the length from the snout to the end of the shortest rays in the fork of the tail).

The SCUs were left untouched until February 1987. At this time all planktivorous fish, including humbugs, that had settled to the SCUs from the plankton were removed. The three recruit density treatments were then established, and the experiment started, by collecting newly settled humbugs and transplanting them

TABLE 1. Description of experimental factors and design. Treatments consisted of all possible combinations of the four factors. Two replicate standard coral units (SCUs) were assigned at random to each treatment combination ($n = 72$ SCUs).

Factor	Fixed/random	Levels
Initial recruit density	F	low, medium, and high (2, 7, and 14 recruits per SCU, respectively)
Presence of adults	F	present vs. absent (3-4 vs. 0 adults per SCU)
Food supplementation	F	yes vs. no (SCU supplied with extra food, vs. natural food only)
Sites	R	sites 1, 2, and 3

to the cleared SCUs at the appropriate densities. Recruits transplanted included individuals collected from *P. damicornis* colonies in other areas of One Tree Reef as well as those removed from the SCUs. Recruits were allocated to SCUs at sites 1, 2, and 3 on 14, 12, and 11 February 1987, respectively.

Newly settled humbugs are 8-9 mm FL at first appearance on the reef (G. E. Forrester, *personal observation*). Recruits transplanted to SCUs ranged from 9 to 13 mm FL (mean = 11.4 mm FL, $s^2 = 1.02$). Most recruits were between 3 and 12 d postsettlement at allocation. All of the recruits allocated to any one SCU were of the same FL. The experiment ran for 10 mo; it was monitored during field trips centered around May and August 1987, and terminated in December 1987.

Food supplementation

The supplemental food was fish flesh, put through a food processor to produce plankton-sized particles. The processed fish was frozen into cubes. From the start of the experiment until early May 1987, all cubes fed were of the same size. Thenceforth the size of cubes fed was proportional to the size of the group, so that the amount of food fed per fish was equal. The fish were fed supplemental food by way of the feeding tubes attached to the SCUs (Fig. 2). The frozen cubes were dropped

TABLE 2. Estimates of recruitment used to choose initial recruit densities. SCUs = standard coral units.

Source of data	Mean density	Range
Recruits accumulated on 72 SCUs to 8 Feb 1987 (Forrester 1988)	5.8*	0-21
Census of recruits on 73 <i>P. damicornis</i> in May 1986 (G. E. Forrester, <i>personal observations</i>)	4.9*	0-28
Census of recruits on 20 <i>P. damicornis</i> in Feb 1984 (Jones 1987b)	4.8	0-10

* Densities of 0 not used in calculation of means as they are irrelevant to estimates of densities that juveniles experience (Jones 1987a).

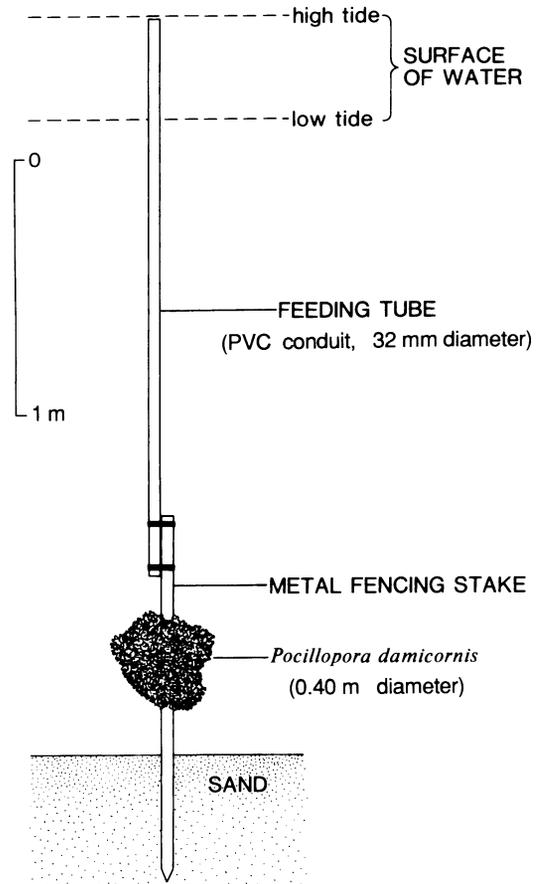


FIG. 2. A diagram showing the construction of a standard coral unit (SCU). PVC = polyvinyl chloride plastic.

into the top of the feeding tubes from a boat. As they defrosted, they broke up and started sinking, emerging from the bottom of the tubes as a stream of particles over a period of 5-12 min. In situ observations revealed that the fish readily consumed this food. The fish were fed during low tide on 78 of the 279 d the experiment ran.

Marking of recruits

A fluorescent mark was made on growth increments in the otoliths (ear stones) of all the recruits to be transplanted to SCUs. Marks were made by immersing the recruits in a solution of tetracycline at a concentration of 0.8 g/L for 24 h before they were allocated to SCUs. For details of this technique see Schmitt (1984). These marks were used to distinguish recruits transplanted to SCUs from other humbugs. They could only be detected in fish that had been killed. To view them the pair of smallest otoliths (asteriscii) was dissected out, mounted on a slide in resin, and examined under ultraviolet light.

The second marking technique used allowed the recognition of individual fish over time while the experiment was running. Liquid latex (Riley 1966) or tat-

toeing dyes (Mapstone 1988) were injected under the fishes' skin to produce colored marks on their sides. Using a variety of colors and marking positions it was possible to give a different mark to most of the fish marked using this technique. Recruits were only marked in this way once they reached 25 mm FL. A pilot study indicated that dye marking does not influence the growth of humbugs > 25 mm FL. Marks on fish smaller than this disappeared too quickly to have been useful, and marking caused increased mortality of very small fish (<17 mm FL) (G. E. Forrester, *personal observation*).

Monitoring

During the May and August field trips, all the recruits were collected from their SCUs and transported to the laboratory where their fork lengths were measured, and they were dye marked if large enough. They were all successfully returned to their SCUs the same day (or occasionally the next day). Thirty-seven juveniles collected were deemed to have settled to the SCUs subsequent to the commencement of the experiment, by virtue of their small size, and were not returned. No juveniles removed in this manner possessed tetracycline-marked otoliths, verifying that they were subsequent recruits and not recruits I had transplanted. Four adults that migrated onto adults-absent SCUs were removed as they were noticed. In December 1987 all humbugs on the SCUs were collected as before, taken back to the laboratory and killed using rotenone. They were measured (FL), and all dye marks were noted. Their gonads were removed, and their otoliths checked for tetracycline marks.

Assessment of rates of demographic processes

At the beginning and end of each field trip all natural corals within 30 m of the experimental sites were checked for the presence of dye-marked humbugs that had emigrated from experimental SCUs. When the experiment was terminated the humbugs were collected from seven of these corals and their otoliths later checked for tetracycline marks. Instances of migration, either among SCUs or between SCUs and natural corals, were inferred by way of the regular checks of the location of dye-marked recruits during the experiment and by the distribution of tetracycline-marked individuals at the end of the experiment. Excepting those settlers from the plankton that were removed, humbug recruits that immigrated to SCUs during the experiment were considered part of the group from that point on for the purposes of calculating all variables except mortality rates.

All dye-marked recruits that disappeared and were not subsequently found at another site were assumed to have died. For non-dye-marked recruits, I assumed that if numbers in a group remained constant then no mortality had occurred and that all reductions in numbers were due to mortality and not migration. Survival

rates were calculated as the proportion remaining after a given time period.

Dye marking the recruits in May had effectively separated them into two size classes, <25 mm FL (non-dye-marked) and >25 mm FL (dye-marked). As a crude test for size-dependence of apparent mortality, for all groups where there were fish in both size categories, I calculated the proportion of recruits in each class that disappeared before December.

Growth rates of recruits were calculated as changes in absolute size (FL). Two variables were considered to examine the effects of the experimental treatments on growth rates: the mean growth increment (GI) for the members of each group over a given time interval (group GI), and the growth increment of the dominant (largest) juvenile in each group (dominant GI). Between February and May, since all the fish started out at the same size, group GIs were calculated as the change in mean size over this period. For May–August and May–December group GIs could only be estimated because the fish were of different initial sizes and because individual GIs were not attainable for non-dye-marked recruits. On these occasions, for each group, I first calculated the individual GI of every dye-marked juvenile that was present at the beginning and the end of the interval. I then estimated the mean growth increment of the non-dye-marked recruits present at the beginning of the interval, as the difference between their mean size and the mean size of the non-dye-marked recruits present at the end. The average of all of the increments was then taken to give an estimated group GI.

The state of maturity of the humbugs removed from the SCUs in December was assessed on the basis of the external appearance of their gonads when they were dissected. Histological examination of a sample of these gonads verified that this method of assessment was accurate (Forrester 1988).

Analyses

Hypotheses about effects of the experimental factors on demographic variables were tested using analyses of variance (ANOVA). Prior to analysis data were tested for heteroscedasticity using Cochran's test (Underwood 1981). When variances were heterogeneous ($P < .05$ for Cochran's test) analyses were performed on data transformed to be homoscedastic.

All analyses used the same model, where the four experimental factors were orthogonal and SCUs constituted replicates. All factors were considered fixed except "sites," which was considered random (Table 1). Since the degrees of freedom associated with each term and the protocol for calculation of F ratios was the same for all analyses (with one exception; see Table 5) a full ANOVA table is presented only for the first such analysis as an example (Table 4 below). For subsequent analyses only F ratios and P values judged significant are presented. Post-hoc pooling procedures,

TABLE 3. Instances of confirmed migration by small (<25 mm fork length [FL]) and large (>25 mm FL) juveniles over different time intervals during the experiment and overall (Total).

Time period	Between SCUs*		From SCUs to natural corals		From natural corals to SCUs	
	Small	Large	Small	Large	Small	Large
Feb-May	0	0	0	0	0	0
May-Aug	0	1	0	2	0	1
Aug-Dec	0	2	0	4	1?	1
Total	0	3	0	6	1	2

* Standard coral units.

as described by Winer (1971), were sometimes used to remove nonsignificant terms from the model to allow more powerful tests of the remaining terms. In only one case did this alter the conclusions drawn from an analysis. A full ANOVA table is presented for this analysis (Table 5 below).

RESULTS

Migration rates

Very few instances of migration were detected (Table 3). The proportion of recruits found to have migrated during the experiment was 0.022. Confirmed movements were so few that analysis of effects of the experimental factors on migration would not be meaningful.

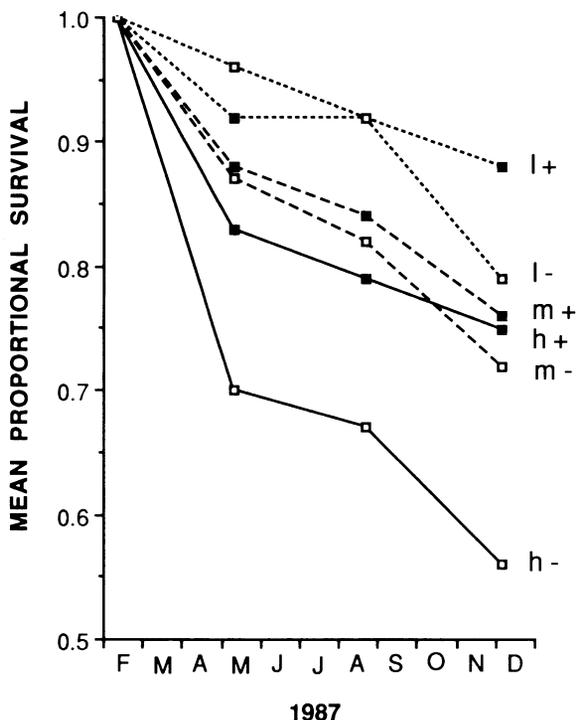


FIG. 3. Mean survival over 10 mo of recruits at three different initial densities (h = 14, m = 7, l = 2 recruits per SCU), in the presence (+ = 3-4 adults per SCU) and absence (-) of adults. (n = 12 SCUs per point).

Mortality rates

The proportion of recruits that disappeared and were not shown to have migrated was 0.257. Apparent mortality was generally highest during the first part of the experiment (February-May) and lowest during the winter months (May-August) (Figs. 3 and 4). Apparent mortality from February to May was greatest on SCUs having high densities of recruits but no adults present (Fig. 3), causing a significant interaction between the density of recruits and the presence of adults (Table 4). Apparent mortality also differed significantly among sites (Table 4), being more than twice as great at site 2 as at sites 1 and 3 (Fig. 4).

Apparent mortality data for May-August and August-December were very heteroscedastic ($P < .0004$ for Cochran's test) and were not equalized by any of four transformations tried (P always $< .01$ for Cochran's test). The results of an analysis of apparent mortality over the whole experiment were not very different from those from February-May (Table 5, Figs. 3 and 4). This suggests that any effects of the experimental factors from May to December were either similar in kind to those established during the initial 3 mo or, if different, not strong enough to cancel them out. Apparent mortality over the whole experiment declined significantly with increasing recruit density (Table 5, Fig. 3) and may have been lower in the presence of adults (mean \pm SE = 0.194 ± 0.030) than in their absence (0.276 ± 0.039) (Table 5). Recruits at site 2 continued to suffer significantly greater apparent mortality than those at the other two sites (Table 5, Fig. 4).

Apparent mortality from May to December was strongly size dependent. Very few large recruits (>25 mm FL) disappeared during this period (proportion = 0.028). Virtually all mortality was of small (<25 mm FL) recruits (proportion = 0.165). This difference was statistically significant (Wilcoxon signed-ranks test, $Z_{56} = 4.115$, $P = .00004$).

Growth rates

Growth from February to May was very rapid, and most recruits at least doubled in size during this time (mean FL at allocation = 11.4 mm, mean FL in May = 25.3 mm). There were huge differences among individual growth rates within groups and by May in-

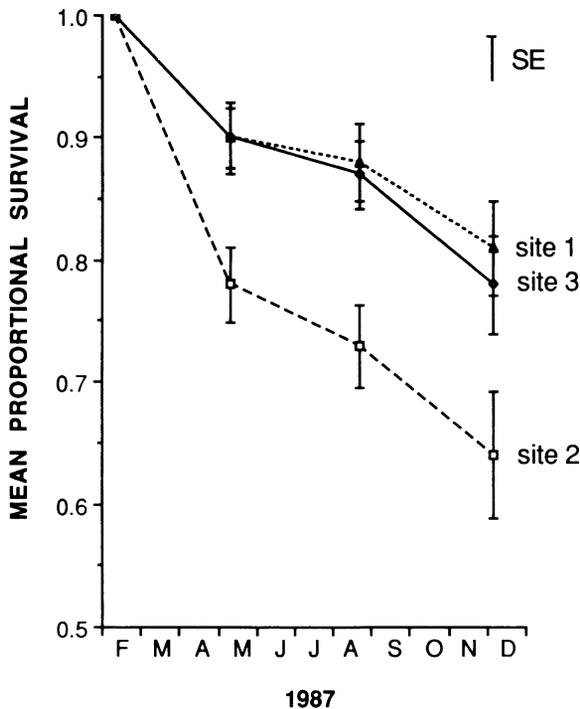


FIG. 4. Survival over 10 mo of recruits on 24 standard coral units (SCUs) at each of three different locations (sites 1, 2, and 3; means \pm 1 SE).

dividuals within most groups were regularly graded in size (e.g., Fig. 5). Where individually recognized recruits were followed over time, in no instance did a juvenile grow to overtake another group member in size (e.g., Fig. 5). This suggests that once size hierarchies were established, they were maintained. Growth over the winter months (May–August) was very slow (mean GI = 3.14 mm, $s^2 = 0.35$), and variation in individual growth rates was very low, reflected by the

TABLE 4. Analysis of variance on proportional survival of recruits over the first third of the experiment (between February and May 1987) (Cochran's $C = 0.2017$, $P = .210$).

Source	Sum of squares	df	Mean square	F	P
Density (D)	0.38024	2	0.19012	13.28	.017
Adults (A)	0.02048	1	0.02048	2.979	.226
Food (F)	0.00064	1	0.00064	0.049	.845
Sites (S)	0.22123	2	0.11061	6.424	.004*
D \times A	0.09368	2	0.04684	9.055	.033*
D \times F	0.03104	2	0.01552	1.177	.396
D \times S	0.05726	4	0.01431	0.831	.514
A \times F	0.02048	1	0.02048	0.941	.434
A \times S	0.01375	2	0.00687	0.399	.674
F \times S	0.02594	2	0.01297	0.753	.478
D \times A \times F	0.08177	2	0.04089	1.682	.295
D \times A \times S	0.02069	4	0.00517	0.300	.876
D \times F \times S	0.05272	4	0.01318	0.765	.555
A \times F \times S	0.04351	2	0.02175	1.263	.295
D \times A \times F \times S	0.09722	4	0.02431	1.412	.250
Residual	0.61990	36	0.01722		

* F ratios interpreted as significant.

TABLE 5. Analysis of variance on proportional survival of recruits over the whole experiment (between February and December 1987).† Results are presented after pooling of terms for which P was $>.25$ (Winer 1971).

Source	Sum of squares	df	Mean square	F	P
Density (D)	0.05587	2	0.02794	7.403	<.005*
Adults (A)	0.01262	1	0.01262	3.344	.07
Sites (S)	0.03390	2	0.01670	4.425	<.025*
D \times A \times S	0.02537	4	0.00634	1.682	>.1
A \times Food \times S	0.01450	2	0.00725	1.923	>.1
Residual	0.02340	62	0.00377		

* F ratios interpreted as significant.

† Data were heteroscedastic (Cochran's $C = 0.3506$, $P = .005$), so the analysis was performed on data transformed to $\log_{10}(x + 1)$ (Cochran's $C = 0.2797$, $P = .035$).

low variance around the mean. Growth rates rose again from August–December (mean GI = 7.08 mm, $s^2 = 1.99$). Variation within groups in the final sizes reached by recruits was much greater at high densities; this was because the fastest growing recruits grew to roughly similar sizes at all densities, but at high densities many of the recruits grew very slowly (e.g., Fig. 5).

The size dependence of apparent mortality probably introduced some bias in the estimated mean growth increments (group GIs). All else being equal, these estimates will tend to be biased upwards on SCUs where there was mortality of non-dye-marked juveniles. From August to December most of the juveniles were marked so the potential for the bias to affect the estimate was quite small. The potential bias was greater from May to August because a greater proportion of the juveniles were not dye marked, but growth was so slight and showed so little variation among individuals that any bias was probably not important.

Effects of the experimental factors on growth were very complex. From February to May all four factors were involved in interactive effects on group GIs (Table 6A). The comparisons of means (Table 6B) were interpreted as follows. The presence of adults reduced growth, but this effect was less at site 2 than at sites 1 and 3. Supplemental feeding generally increased growth rates. The effect of feeding did not occur in the presence of adults and was reduced at site 2 compared to the other two sites. Growth rates increased as density decreased, and the effect of adults to reduce growth increased as density decreased. The enhancement of growth by feeding became greater at lower densities. In terms of the magnitudes of the differences between the means, the effects involving adults and sites seem to be smaller than those involving food and density (Table 6B).

Feeding had no effect on growth between May and August (Table 6A). There was a general tendency for group GIs to decrease as recruit density increased (Table 6B). This trend was modified in two specific instances, resulting in a significant interaction term in

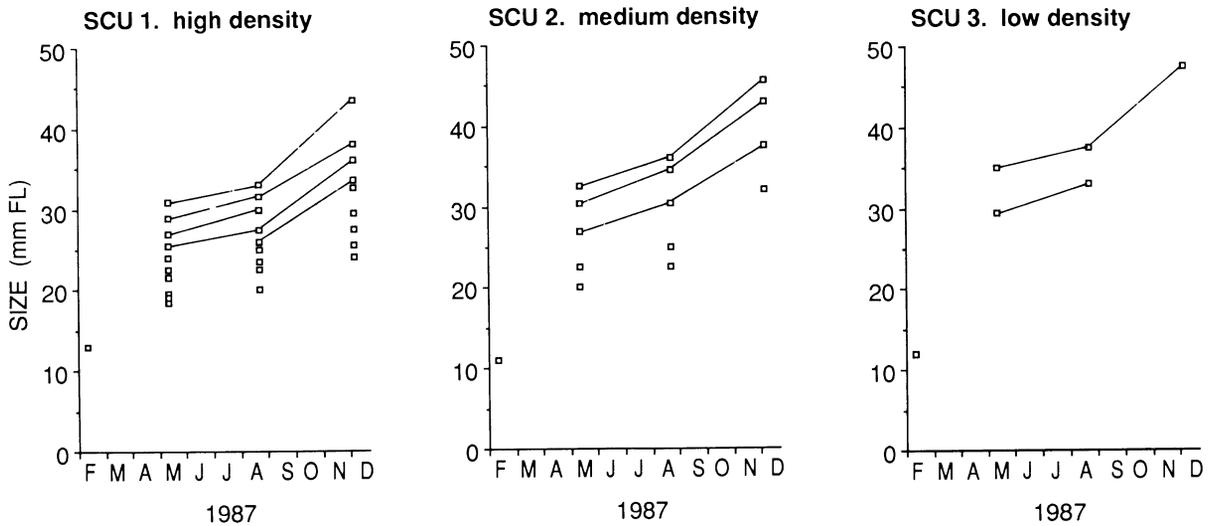


FIG. 5. Growth of individual recruits. Plots showing the sizes of the recruits present on three of the standard coral units (SCUs) at different times during the experiment. The three SCUs had different initial densities of recruits, high (=14), medium (=7), and low (=2) numbers of recruits per SCU, but were otherwise subject to the same experimental treatments. The SCUs were at site 1, received no supplemental food, and did not contain adults. Lines indicate the recognition of marked individuals over time.

the ANOVA (Table 6A). These instances were both at medium density, first at site 1 where adults were present and secondly at site 2 in the absence of adults (Table 6B). The absolute differences between means are very small compared to those observed from February to May, reflecting the generally slow growth over this period.

From August to December recruits again grew significantly faster at lower densities (Table 6A). Mean (\pm SE) group GIs were 6.47 (\pm 0.24) at high density, 6.89 (\pm 0.28) at medium density and 7.89 (\pm 0.28) at low density. Mean growth was also significantly enhanced by supplemental feeding (Table 6). The mean (\pm SE) group GI with supplemental feeding was 7.85 (\pm 0.21) and the mean GI without feeding was 6.31 (\pm 0.19).

During the first two-thirds of the experiment the experimental factors had effects on the growth of the dominant juvenile (dominant GI) broadly similar to those on mean growth of the group. From February to May there were complex interactive effects involving all of the experimental factors, resulting in a significant four-way interaction term in the ANOVA ($F = 2.749$, $P = .043$). From May to August there was an interactive effect of recruit density, presence of adults and sites similar to that for the group GI ($F = 2.963$, $P = .033$).

From August to December group GIs declined with increasing recruit density. In contrast dominant GIs were greater at high density (mean \pm SE = 8.31 ± 0.42) than at medium and low densities (6.94 ± 0.40 and 7.19 ± 0.33 , respectively) ($F = 18.04$, $P = .010$). Group GIs did not differ significantly in the presence and absence of adults. Dominant GIs, however, were significantly lower on SCUs where adults were present (mean

\pm SE = 6.15 ± 0.14) than on those where they were absent (8.81 ± 0.25) ($F = 172.9$, $P = .006$).

Modification of recruitment patterns

The factors influencing the number of recruits present on SCUs in December were the same as those influencing apparent mortality (Table 7). There were significantly fewer recruits present on SCUs at site 2 than at sites 1 and 3, where numbers were not significantly different (Fig. 6A). There was a tendency for more recruits to be present on SCUs with adults present. This tendency increased with increasing initial recruit density (Fig. 6C). The three levels of recruit density set up in February still remained distinct in December, though the absolute differences between the three treatments did decrease (Fig. 6C).

The mean size of the recruits remaining at the end of the experiment reflects the influence of differences in growth plus the effect of size-dependent mortality. Apparent mortality and growth were affected by different factors in different ways, and perhaps for this reason the influence of the experimental factors on this variable was very complex. The analysis of variance (Table 7) suggests that there were effects of density and adults that interacted with each other, and also interacted separately with effects of feeding and sites. Multiple comparison tests indicated that generally mean size was reduced in the presence of adults and at increasing recruit densities and was increased by supplemental feeding, but that these effects were modified in several ways. In terms of the magnitude of differences among means those effects involving density were generally the greatest (Table 8).

TABLE 6. Summary of results of analyses of variance on the effects of the experimental factors on mean growth increments. For February–May 1987 Cochran's $C = 0.2564$, $P = .057$; for May–August 1987 Cochran's $C = 0.1149$, $P = 1.000$; for August–December 1987 Cochran's $C = 0.1730$, $P = .407$.

Source	Feb–May		May–Aug		Aug–Dec	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Density	2587	.000	39.62	.002	0.872	.001*
Adults	13.38	.067	0.551	.535	9.888	.088
Food	15.65	.058	5.266	.149	20.683	.000*
Sites	2.918	.067	0.518	.600	0.872	.427
D × A	9.083	.033*	0.521	.629	2.974	.162
D × F	9.521	.030*	0.089	.916	1.760	.283
D × S	0.090	.985	0.623	.649	0.343	.847
A × F	12.10	.074*	3.363	.208	4.369	.172
A × S	4.364	.020*	1.133	.333	2.373	.108
F × S	4.450	.019*	0.332	.720	0.003	.997
D × A × F	1.242	.381	0.424	.680	1.757	.283
D × A × S	1.418	.248	2.963	.033*	2.009	.114
D × F × S	0.835	.512	1.148	.350	1.645	.184
A × F × S	0.806	.454	0.209	.812	0.544	.585
D × A × F × S	1.057	.392	1.877	.136	1.857	.139

B) Comparison of mean growth increments for significant interactions using SNK tests. Means sharing a common underline are not significantly different at $P < .05$.

February–May						
Density	high	high	medium	medium	low	low
Feeding	unfed	fed	unfed	fed	unfed	fed
Mean	<u>11.04</u>	<u>12.15</u>	<u>12.31</u>	<u>13.63</u>	<u>15.65</u>	<u>18.71</u>
Density	high	high	medium	medium	low	low
Adults	present	absent	present	absent	present	absent
Mean	<u>11.26</u>	<u>11.93</u>	<u>12.40</u>	<u>13.54</u>	<u>15.56</u>	<u>18.79</u>
Adults	present	present	present	absent	absent	absent
Sites	3	1	2	2	3	1
Mean	<u>12.82</u>	<u>13.19</u>	<u>13.22</u>	<u>13.98</u>	<u>14.97</u>	<u>15.31</u>
Feeding	unfed	unfed	unfed	fed	fed	fed
Sites	3	1	2	2	3	1
Mean	<u>12.92</u>	<u>12.97</u>	<u>13.11</u>	<u>14.09</u>	<u>14.87</u>	<u>15.53</u>
Adults	present	absent	present	absent		
Feeding	unfed	unfed	fed	fed		
Mean	<u>12.50</u>	<u>13.50</u>	<u>13.65</u>	<u>16.01</u>		
May–August						
Site 1						
Density	medium	high	high	medium	low	low
Adults	present	absent	present	absent	present	absent
Mean	<u>2.39</u>	<u>2.73</u>	<u>2.85</u>	<u>3.17</u>	<u>3.62</u>	<u>3.69</u>
Site 2						
Density	high	medium	high	medium	low	low
Adults	present	absent	absent	present	absent	present
Mean	<u>2.67</u>	<u>2.80</u>	<u>2.99</u>	<u>3.40</u>	<u>3.63</u>	<u>3.75</u>
Site 3						
Density	high	high	medium	medium	low	low
Adults	present	absent	absent	present	absent	present
Mean	<u>2.28</u>	<u>3.06</u>	<u>3.10</u>	<u>3.12</u>	<u>3.44</u>	<u>3.75</u>

The size-frequency distributions of mature and immature recruits removed from the SCUs in December are displayed in Fig. 7. There was a strong correlation between size and reproductive status. No recruits < 36.5 mm FL became mature. The mean number of recruits that became mature was significantly increased under supplemental feeding (Table 7, Fig. 6B). There was also

a reduction in numbers maturing in the presence of adults (Table 7, Fig. 6C). There may have been an effect of density (Table 7), but the differences in numbers between the three levels were tiny compared to the differences in the number of recruits allocated in February. The number of recruits becoming mature was largely unrelated to the initial density (Fig. 6C). There

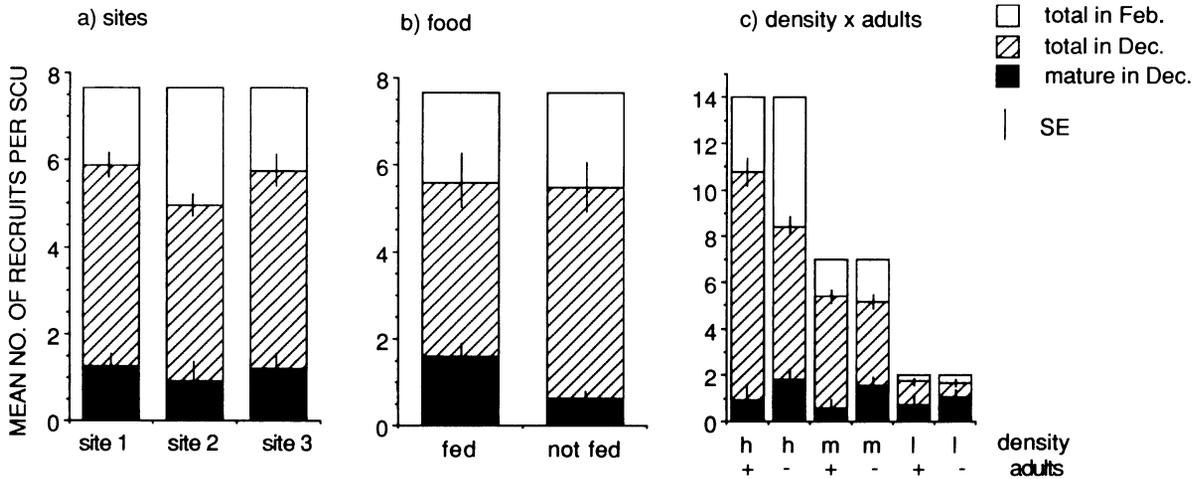


FIG. 6. Modification of a pattern of (artificial) recruitment. Plots show numbers of recruits initially transplanted to standard coral units (SCUs) in February 1987 (open portions of bars), the mean numbers remaining in December 1987 (hatched), and the mean numbers of those that became sexually mature (solid). The three plots show differences among sites (a), the effect of supplemental feeding (b), and the interactive effects of initial recruit density and the presence of adults (c). For plot (c), symbols on the x-axis refer to the levels of initial recruit density (h = 14, m = 7, and l = 2 recruits per SCU) and the presence (+) and absence (-) of adults.

were no differences among the three sites in the number of recruits becoming mature (Table 7, Fig. 6A).

DISCUSSION

Demography of juvenile humbugs

Migration.—The contribution of postsettlement dispersal to changes in abundance has usually not been measured for coral reef fishes (Doherty 1982, 1983, Jones 1987a, b, 1989). In this experiment migration was apparently too infrequent to influence abundance. This may have been because of the large distance (20 m) separating SCUs since Jones (1987b) and I (*personal observation*) have inferred substantial movement of humbugs among *Pocillopora* corals separated by 10 m

and 4–11 m, respectively. Migration may also be more important on other coral species. Sparsely branching *Acropora* corals support large populations of adult humbugs at One Tree Reef, but I have never observed recruitment to these corals, possibly because the branches are too widely spaced to provide adequate shelter for recruits. This population is presumably maintained entirely by immigration of individuals that originally settled elsewhere. Migration thus warrants further attention, especially in species that are less habitat specific and more mobile than humbugs. Robertson (1988), for example, found migration to be important in redistributing recruits of three such species of surgeonfish.

Survival.—Humbugs are the only species of coral-

TABLE 7. Results of analyses of variance on the effects of the experimental factors on the number of recruits present on SCUs in December, their mean size (FL) and the number that had become mature. For number present Cochran's *C* = 0.2286, *P* = .112, for mean size Cochran's *C* = 0.1728, *P* = .410, for number mature Cochran's *C* = 0.257, *P* = .056.

Source	Number present		Mean size		Number mature	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Density	193.2	.000	151.1	.000	6.200	.059*
Adults	36.57	.026	23.83	.039	12.79	.070*
Food	0.108	.774	84.94	.012	25.00	.038*
Sites	7.086	.003*	1.592	.217	1.629	.210
D × A	9.700	.029*	10.70	.025*	1.727	.288
D × F	1.872	.267	1.741	.286	0.392	.699
D × S	1.985	.118	2.993	.031	0.429	.787
A × F	0.750	.478	3.483	.203	0.510	.549
A × S	0.400	.673	4.412	.019	1.629	.210
F × S	2.114	.135	2.228	.122	1.400	.260
D × A × F	0.740	.533	5.468	.072	2.714	.180
D × A × S	1.000	.420	1.734	.164	0.943	.450
D × F × S	0.786	.542	3.858	.010*	2.257	.082
A × F × S	0.686	.510	6.623	.004*	1.400	.260
D × A × F × S	2.143	.095	1.443	.240	0.200	.937

* *F* ratios interpreted as significant.

TABLE 8. Mean sizes of recruits on standard coral units (SCUs) at the end of the experiment under different experimental treatments. Initial densities of recruits were 2 (= Low), 7 (= Medium), and 14 (= High). Adults were present (= Pres.) or absent (= Abs.). SCUs were or were not supplied with supplemental food.

Supple- mental feeding? Site	Initial recruit density					
	High		Medium		Low	
	Pres.	Abs.	Pres.	Abs.	Pres.	Abs.
Yes 1	32.7	34.5	34.2	38.3	40.3	45.8
Yes 2	33.0	31.8	35.0	36.0	40.0	44.9
Yes 3	32.8	34.6	34.8	39.7	38.0	47.1
No 1	31.7	32.1	30.4	33.4	38.1	39.4
No 2	31.7	31.2	33.1	34.5	35.9	39.0
No 3	29.0	30.7	33.4	33.4	38.6	39.6

reef fish for which density-dependent mortality has been consistently detected. Jones (1987b, 1989) found, as I did, that the apparent mortality of juveniles was positively related to their density. Apparent mortality of the two other damselfish species tested to date, *Pomacentrus amboinensis* (Jones 1987a) and *P. wardi* (Doherty 1982, 1983) was affected very slightly, or not at all, by density.

In contrast to the negative intracohort effect, the presence of adults tended to enhance the survival of recruits (see also Jones 1987b). This effect would seem not to be resource related because of the negative effect of adults on growth and their restriction of juveniles access to certain prey types (Coates 1980a, G. E. Forrester, *unpublished manuscript*). Members of humbug social groups retreat simultaneously into their home coral when threatened. Adults swim farther from the home coral and cover larger areas than juveniles (Coates 1980a, G. E. Forrester, *unpublished manuscript*). They may thereby increase group vigilance (Bertram 1978) and reduce the susceptibility of juveniles to predation (Pulliam and Caraco 1984, Pitcher 1986). Adults are also highly aggressive towards potentially predatory species (Coates 1980b) and might reduce predation on juveniles by driving potential predators away.

The larger scale differences among sites in apparent mortality of recruits were independent of the within-group effects of adults and density. Again one can only speculate as to the reason for these differences. Site 2, where apparent mortality was highest, was surrounded by more contiguous reef than the other two sites. Large piscivorous species are more common on such reefs. The difference may thus be due to differences in predation pressure. Differences in mortality rates at similar scales have been detected for other reef fishes (Aldenhoven 1986, Robertson 1988).

It has been argued that studies on small patches of habitat such as this are not representative of events occurring on larger reefs (Ogden and Ebersole 1981). This criticism does not apply strongly to humbugs since small isolated corals are their primary natural habitat. In addition, apparent mortality rates of recruits on

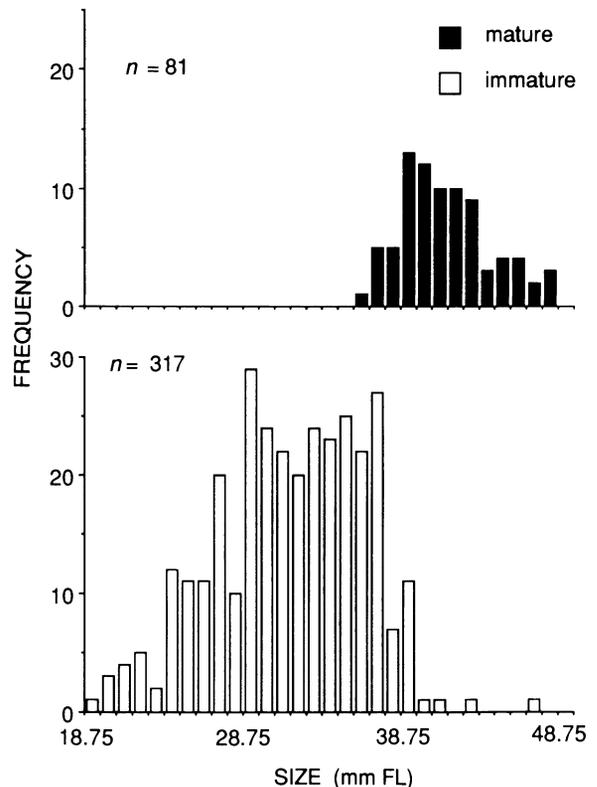


FIG. 7. Size-frequency distributions of mature and immature recruits present on standard coral units (SCUs) at the end of the experiment.

SCUs are in accord with the limited data available on disappearance rates on natural corals (Sale and Ferrell 1988), suggesting that any artifacts associated with the use of SCUs were not extreme. Examining effects of density at the scale of individual corals is appropriate since this is the scale at which individuals directly experience density. Density dependence at this scale may not be detected by studies averaging across sites (Hassell 1986).

Growth.—A notable feature of the effects of the experimental factors on growth rates was their complexity. Most effects were interactive and also changed during the course of the experiment. Another notable feature was that the factors influencing growth were often different to those influencing apparent mortality. Though there were differences in apparent mortality, there were no consistent differences among sites in growth rates of recruits. Supplemental feeding had complex but always positive effects on growth rates, but no measured effect on survival. The reduction in mean growth of recruits by adults during the first third of the experiment stands in contrast to their positive effect on recruit survival.

Strong regulatory effects on growth rates have been a consistent finding of recent studies of fishes on tropical (Doherty 1982, Jones 1987a, 1989) and temperate reefs (Jones 1984, Ochi 1986) and are widespread

among fish populations (Backiel and LeCren 1978). The only studies on coral reefs not detecting regulatory effects on growth are Jones' (1987*b*, 1989) experiments on humbugs. He reported mean size attained by juveniles to be independent of both their own and adult density. This difference in results may reflect intraspecific variation in regulatory effects or differences in experimental procedure.

Fishes show very plastic growth. It therefore seems likely that the first response to crowding would be a reduction in growth, rather than outright mortality. The nature of the effects of adults and density was qualitatively similar to those observed in many plant populations. Shading by adults restricts the growth of juveniles of many tree species (Brokaw 1985) and giant kelp (Dean and Jacobsen 1984). Where there are no adults and seedlings are planted at different densities, the first response to crowding is a decrease in mean size with increasing density (e.g., Donald 1951). As well as an increase in the mean, there was also an increase in the variance of mean size of recruits during this experiment. This is known as growth depensation (Magnuson 1962). The increase in variance was greater at higher densities. Again, similar size hierarchies where size-frequency distributions become positively skewed over time and the degree of skewing increases with increasing density form in even-aged stands of some plants (e.g., Obeid et al. 1967).

The complexity of the effects on growth raises the question of the mechanisms responsible for these effects, and in particular whether the interactions among recruits and between recruits and adults are related to a shortage of food or to direct effects of crowding. Augmentation of natural food resources has revealed food limitation of various animal populations (e.g., Wise 1975, Jansson et al. 1981, Taitt 1981). It should be noted, however, that in the absence of knowledge of natural resource levels or consumption rates, failure to detect a response is an ambiguous result. It may arise either because food was not limiting or because the amount fed was simply not enough to cause a response. I am, therefore, restricted to concluding that food limitation was detected during the first and final thirds of the experiment.

Shortages of food may be relative or absolute (=competitive, *sensu* Andrewartha and Birch 1954). During the first third of the experiment the enhancement of the growth of recruits under supplemental feeding was conditional on both their density and the presence of adults. The increase in the degree of enhancement as recruit density decreased suggests within-group competition among recruits (Underwood 1979). This result, however, may also be an artefact of the feeding method since during this time the same amount of food was supplied to groups, so smaller groups would have received more food per individual. Over the same period, the release of growth of recruits with feeding did not occur in the presence of adults. This is likely due

to competition with adults. Unquantified observations during feeding sessions indicated that adults were taking up position close to the source of the supplemental food, and may have reduced the juveniles' access to it by keeping them farther away. Similar interactions occur between adults and juveniles feeding on natural food (Coates 1980*a*, G. E. Forrester, *unpublished manuscript*). The enhancement of growth by feeding during the final third of the experiment was independent of other factors and so presumably reflects a shortage in the supply to groups. This shortage was either relative or due to competition at larger scales, for example, by reduction in the supply of food by planktivores feeding in upstream areas (Bray 1981).

Direct social inhibition of growth at high densities when food is in excess has been demonstrated in fish (Abbott and Dill 1989) and other aquatic vertebrates (Rose and Rose 1965, Licht 1967). At least some of the effects of density and adult presence on the growth of recruits seem likely to be the result of hierarchical interactions within groups. The lack of overtaking in size and the selective retardation of the growth of the largest juveniles towards the end of the experiment in the presence of adults are consistent with this interpretation.

In plant populations, inhibition of juvenile growth by adults and the formation of the type of size hierarchy observed in juvenile humbugs are usually attributed to asymmetric competition for light (Weiner and Thomas 1986). Asymmetric competition for food within groups may explain their occurrence in this experiment, although direct inhibition of growth as a product of dominance interactions is also likely to have contributed.

Limitation of population size

There have been some conceptual differences in the reef fish literature regarding the definition of the recruitment limitation model (Warner and Hughes, *in press*). Recruitment limitation is usually defined as the absence of resource limitation or competitive effects on population size (Sale et al. 1984, Victor 1986). In addition, some authors have specified that there should be no density-dependent effects on processes that affect abundance (Doherty 1982, 1983, Doherty and Williams 1988, Mapstone and Fowler 1988). Since density dependence may result from other factors such as predation (Holling 1959) and parasitism (Anderson 1979) as well as competition, it may occur in a recruitment-limited population. I would therefore suggest dropping the criterion of density dependence as necessary and sufficient evidence against recruitment limitation.

Population studies on coral reef fishes may be divided into those that have focused on making predictions about all reef-associated individuals (=total population) (Doherty 1981, 1982, 1983, Doherty and Williams 1988) or only those reef-associated individuals that are sexually mature (=adult population) (Victor 1983, 1986, Jones 1987*a*, Shulman and Ogden 1987,

Robertson 1988). I see no reason for preferring one of these definitions over the other. Here I will consider both total and adult populations because appreciation of how factors influencing demography change with ontogeny should lead to a better understanding of reef fish populations.

The results suggest that total population size is not food limited since supplemental feeding had no measurable influence on the abundance of the recruits. This conclusion is made cautiously, however, since if the experiment had continued for longer the limitation of growth rates by food availability might have been translated into a reduction in survival because of the increased mortality rate of smaller juveniles. The results suggest different conclusions about the limitation of adult density. The number of recruits becoming mature by the end of the experiment was limited by the presence of adults and food availability rather than initial recruit density. This limitation was probably a result of a combination of reduced growth due to a shortage of planktonic food and direct hierarchical inhibition of growth and maturation. One can envision a scenario, equivalent to that in some tree populations (Brokaw 1985), where individuals may recruit into the population and persist as suppressed juveniles for long periods, whereas adult density is strongly limited.

This model may apply to *P. amboinensis*, another planktivorous damselfish that lives in groups (Jones 1986, 1987a), but need not apply to all species. Indeed, given the tremendous range of habits of coral reef fishes, it is almost to be expected that different factors will limit populations of different species. A constructive approach in future would be to attempt more restricted generalizations about limiting factors. For example, are all schooling planktivores likely to be food limited? Are territorial species more likely to be limited by space?

A more pluralistic approach may also be fruitful for studies of single species. Barnacles (Roughgarden 1986) and giant kelp (Nisbet and Bence 1989) are suggested to be both resource limited and recruitment limited in different areas. Settlement is low at One Tree Reef relative to many other areas on the Great Barrier Reef (Sale et al. 1984, Doherty and Williams 1988). The significance of this observation for the limitation of population size in these areas has not yet been established. Limiting factors can be difficult to isolate using descriptive studies (Warner and Hughes, *in press*) and are best identified by experiments where the postulated limiting factors are manipulated (Krebs 1985). Inductive generalizations about larger scale patterns in the operation of different limiting factors must await further experimental studies on a range of species in different locations.

Determination of population size

The role of settlement and postsettlement demographic processes in determining abundance depends on the balance of their relative variability. This ex-

periment does not deal with these processes in unmanipulated populations so I am limited to making suggestions as to the potential role of the experimental factors in controlling abundance.

At the scale of individual corals the negative effect of recruit density and the positive effect of adults on apparent mortality modified the pattern of initial recruit density to some extent. Contrary to prior suggestions (Connell 1985, Victor 1986, Doherty and Williams 1988), the effect of demersal mortality on abundance does not necessarily hinge on whether it is density dependent or density independent. Because losses were slight relative to the differences in recruit density I set up, and to those occurring naturally (Table 1), there was little potential for extreme modification of the recruitment pattern that I set up, and it was largely intact at the end of the experiment. This result is supportive of the recruitment determination model for total population size, but caution is again necessary because this experiment only considered the fate of one cohort for 1 yr. Consideration of a series of annual recruitment events might result in greater modification of cohort strength because if, as the results suggest, juveniles cannot grow to overtake each other in size, the rate at which a recruit can grow will be limited by the size and growth of the fish above it in the group. Where small juveniles (perhaps slow-growing recruits of previous years) are already present, the growth of new recruits may be socially restricted almost immediately. In this situation, density dependence of recruit survival may be more severe because of the increased mortality rate of small juveniles. At a larger scale the differences among the sites in mortality rates of recruits resulted in a lower abundance of recruits at site 2 by the end of the experiment. Thus, at both the scale of individual corals and local sites, the size of the total population will not be entirely recruitment determined.

If attention is focused on the adult population, the results suggest a much greater modification of recruitment patterns. At the scale of individual corals the proportional reduction in numbers maturing in the presence of adults was pronounced, suggesting a potentially important internal regulation of adult density. Likewise, the number of recruits reaching maturity was more than doubled by supplemental feeding. Interpretation of the size of this effect, however, is not possible because of the nature of the test for food limitation (see *Discussion: Limitation of population size* above). The number of recruits that became mature under the different initial density treatments was very low, and constant relative to the numbers of recruits allocated, and the level of artificial recruitment had almost no influence on entry to the adult population after a year. If, however, juveniles do persist in the population for long periods after a period of high settlement the long-term influence on adult density may be difficult to predict.

The relative contribution or importance (*sensu* Wel-

don and Slauson 1986) of settlement and postsettlement processes may be measured by descriptive studies measuring one or both in conjunction with variation in abundance (for a good example see Yoshioka 1982). Experiments such as this one are good for identifying the effects of specific factors on demographic processes at different stages in the life cycle. There may be some difficulty in assessing the importance of these factors in determining abundance. One of the notable features of this study was that the effects of different factors were not additive. The influence of a new factor being measured, say predation on juveniles, may depend on other factors such as food shortages and the presence of conspecific adults. Consideration of a range of factors is thus more complicated than adding on the effect of each new factor measured. Comparing the size of effects measured in different experiments, such as the actual differences between means and components of variance explained, are not meaningful if the design of the experiments is different. Also, procedures for measuring the size effects are not well established (Mapstone 1988).

Mortality of coral reef fishes in the first few days following settlement is often high (Doherty and Sale 1986, Sale and Ferrell 1988). While the transplanted recruits in this experiment were more recently settled than those used in previous studies of this kind (Doherty 1982, 1983, Jones 1986, 1987a, b, 1989), there is still an urgent need to examine the correlation between settlement and recruitment, measured sometime later. The correlation between the two is not always good in other marine species (e.g., Osman et al. 1989). Low juvenile mortality and the high (78%) persistence of adults transplanted to SCUs suggests that humbugs, and other reef fishes (Munro and Williams 1985, Mapstone 1988), are long lived. There is very little information on demographic processes occurring after the first 1 or 2 yr of reef-associated life. The extrapolation of effects measured at one stage, for example on juvenile mortality, to the abundance of the population as a whole (e.g., Weinberg et al. 1986) requires a background of descriptive data that is not yet available for coral reef fishes.

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LITERATURE CITED

- Abbott, J. C., and L. M. Dill. 1989. The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour* **108**:104–133.
- Aldenhoven, J. M. 1986. Local variation in mortality rates and life-expectancy estimates of the coral reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). *Marine Biology* **92**:237–244.
- Anderson, R. M. 1979. The influence of parasitic infection on the dynamics of host population growth. Pages 245–281 in R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific, Oxford, England.
- Andrewartha, H. G., and L. C. Birch. 1954. *The distribution and abundance of animals*. University of Chicago Press, Chicago, Illinois, USA.
- Backiel, T., and E. D. LeCren. 1978. Some density relationships for fish population parameters. Pages 279–302 in S. D. Gerking, editor. *The ecology of freshwater fish production*. Blackwell Scientific, Oxford, England.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. Page 64–96 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Sinauer, Sunderland, Massachusetts, USA.
- Bray, R. N. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipennis*, a planktivorous reef fish. *United States National Marine Fisheries Service Fishery Bulletin* **73**:815–829.
- Brokaw, N. V. L. 1985. Treefalls, regrowth and community structure in tropical forests. Pages 53–68 in S. T. A. Pickett and T. A. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, London, England.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**:923–943.
- Coates, D. 1980a. Prey-size intake in humbug damselfish *Dascyllus aruanus* (Pisces, Pomacentridae) living within social groups. *Journal of Animal Ecology* **49**:335–340.
- . 1980b. The discrimination of and reaction towards predatory and non-predatory species of fish by humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae). *Zeitschrift für Tierpsychologie* **52**:347–354.
- Coe, W. R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology* **34**:225–229.
- Connell, J. H. 1961. The effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* **31**:61–104.
- . 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**:11–45.
- Davies, P. J., B. M. Radke, and C. R. Robinson. 1976. The evolution of One Tree Reef, southern Great Barrier Reef, Queensland. *Bureau of Mineral Resources Journal of Australian Geology and Biophysics* **1**:231–240.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351–389.
- Dean, T. A., and F. R. Jacobsen. 1984. Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. *Marine Biology* **83**:301–311.
- Doherty, P. J. 1981. Coral reef fishes: recruitment limited assemblages? *Proceedings of the Fourth International Coral Reef Symposium (Manila)* **2**:465–470.
- . 1982. Some effects of density on the juveniles of

- two species of tropical territorial damselfishes. *Journal of Experimental Marine Biology and Ecology* **65**:249–261.
- . 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* **64**:176–190.
- Doherty, P. J., and P. F. Sale. 1986. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* **5**:161–163.
- Doherty, P. J., and D. McB. Williams. 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology Annual Review* **26**:487–551.
- Donald, C. M. 1951. Competition among pasture plants I. Intraspecific competition among annual pasture plants. *Australian Journal of Agricultural Research* **2**:335–376.
- Eckert, G. J. 1987. Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Marine Biology* **95**:167–171.
- Forrester, G. E. 1988. Post-recruitment demographic processes in a coral reef fish: their role in the regulation and determination of population size. Thesis. University of Sydney, Sydney, Australia.
- Hassell, M. P. 1986. Detecting density dependence. *Trends in Ecology and Evolution* **1**:90–93.
- Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* **44**:666–680.
- Hobson, E. S., and J. R. Chess. 1978. Trophic relationships among fishes and zooplankters in the lagoon at Eniwetok Atoll, Marshall Islands. United States National Marine Fisheries Service Fishery Bulletin **76**:133–153.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**:385–398.
- Janssen, C., J. Ekman, and A. Von Bromssen. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* **37**:313–322.
- Jones, G. P. 1984. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). II. Factors influencing adult density. *Journal of Experimental Marine Biology and Ecology* **75**:277–303.
- . 1986. Food availability affects growth in a coral reef fish. *Oecologia* (Berlin) **70**:136–139.
- . 1987a. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* **68**:1534–1547.
- . 1987b. Some interactions between residents and recruits in two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **114**:169–182.
- . 1989. Experimental evaluation of the influence of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **123**:115–126.
- Keough, M. J., and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* (Berlin) **54**:348–352.
- Kingsford, M. J. 1988. The early life history of fish in coastal waters of New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**:463–480.
- Krebs, C. J. 1985. *Ecology: the experimental analysis of distribution and abundance*. Third edition. Harper & Row, New York, New York, USA.
- Lewin, R. 1986. Supply-side ecology. *Science* **234**:25–27.
- Licht, L. E. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. *Ecology* **48**:736–745.
- Ludington, C. A. 1979. Tidal modifications and associated circulation in a platform reef lagoon. *Australian Journal of Marine and Freshwater Research* **30**:425–430.
- Magnuson, J. J. 1962. An analysis of aggressive behaviour, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). *Canadian Journal of Zoology* **40**:313–363.
- Mapstone, B. D. 1988. The determination of patterns in the abundance of *Pomacentrus moluccensis* Bleeker on the southern Great Barrier Reef. Dissertation. University of Sydney, Sydney, Australia.
- Mapstone, B. D., and A. J. Fowler. 1988. Recruitment and the structure of assemblages of fish on coral reefs. *Trends in Ecology and Evolution* **3**:72–77.
- Maxwell, W. G. H. 1968. *Atlas of the Great Barrier Reef*. Elsevier, Amsterdam, The Netherlands.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:730–757.
- Munro, J. L., and D. McB. Williams. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. Proceedings of the Fifth International Coral Reef Congress (Tahiti) **4**:545–578.
- Nisbet, R. M., and J. R. Bence. 1989. Alternative dynamic regimes for canopy forming kelp: a variant on density vague population regulation. *American Naturalist* **134**:377–408.
- Obeid, M., D. Machin, and J. L. Harper. 1967. Influence of density on plant to plant variations in fiber flax, *Linum usitatissimum*. *Crop Science* **7**:471–473.
- Ochi, H. 1986. Growth of the anemonefish *Amphiprion clarki* in temperate waters, with special reference to the influence of setting time on the growth of 0-year olds. *Marine Biology* **92**:223–229.
- Ogden, J. C., and J. P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long term study of a large artificial reef. *Marine Ecology Progress Series* **4**:97–103.
- Osman, R. W., R. B. Whitlatch, and R. N. Zajac. 1989. Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. *Marine Ecology Progress Series* **54**:61–73.
- Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. Pages 294–337 in T. J. Pitcher, editor. The behaviour of teleost fishes. Croom Helm, Beckenham, England.
- Pulliam, H. R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 122–147 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*, Second edition. Blackwell Scientific, Oxford, England.
- Richards, W. J., and K. C. Lindeman. 1987. Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. *Bulletin of Marine Science* **41**:397–410.
- Riley, J. D. 1966. Liquid latex marking technique for small fish. *Journal de Conseil Permanent International Exploration de la Mer* **30**:354–357.
- Robertson, D. R. 1988. Abundances of surgeonfishes in Caribbean Panamá: due to settlement or post-settlement processes? *Marine Biology* **97**:495–501.
- Robertson, D. R., and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *Journal of Experimental Marine Biology and Ecology* **40**:285–298.
- Robertson, D. R., S. G. Sheldon, and J. M. Sheldon. 1981. Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. *Ecology* **62**:1162–1169.
- Rose, S. M., and F. C. Rose. 1965. The control of growth and reproduction in freshwater organisms by specific products. *Internationale Vereinigung für theoretische und angewandte Limnologie, Mitteilungen* **13**:21–35.
- Roughgarden, J. 1986. A comparison of food-limited and space-limited animal competition communities. Pages 492–516 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes.

- Pages 491–518 in P. S. Giller and J. H. R. Gee, editors. Organization of communities past and present. Blackwell Scientific, Oxford, England.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**:337–359.
- . 1978. Coexistence of coral reef fishes—a lottery for living space. *Environmental Biology of Fish* **3**:85–102.
- Sale, P. F., P. J. Doherty, G. J. Eckert, W. A. Douglas, and D. J. Ferrell. 1984. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia (Berlin)* **64**:191–198.
- Sale, P. F., and D. J. Ferrell. 1988. Early survivorship of juvenile coral reef fishes. *Coral Reefs* **7**:117–124.
- Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* **140**:284–322.
- Schmitt, P. J. 1984. Marking growth increments in otoliths of larval and juvenile fish by immersion in tetracycline to examine the rate of increment formation. *United States National Marine Fisheries Service Fishery Bulletin* **82**:237–242.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* **74**:85–109.
- Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series* **39**:233–242.
- Smith, C. L., and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Natural History Museum of Los Angeles County Science Bulletin* **14**:125–170.
- Sweatman, H. P. A. 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *Dascyllus reticulatus*) on coral reefs. *Marine Biology* **75**:225–229.
- . 1985a. The influence of adults of some coral reef fish on larval recruitment. *Ecological Monographs* **55**:469–485.
- . 1985b. The timing of settlement by larval *Dascyllus aruanus*: some consequences for larval habitat selection. *Proceedings of the Fifth International Coral Reef Congress (Tahiti.)* **5**:367–371.
- Taitt, M. J. 1981. The effect of extra food on small rodent populations. I. Deermice (*Peromyscus maniculatus*). *Journal of Animal Ecology* **50**:111–124.
- Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable high-diversity systems? *Ecological Monographs* **49**:425–440.
- Thresher, R. E. 1983. Habitat effects on reproductive success in the coral reef fish, *Acanthachromis polyacanthus* (Pomacentridae). *Ecology* **64**:1184–1199.
- Underwood, A. J. 1979. The ecology of intertidal gastropods. *Advances in Marine Biology* **16**:111–210.
- . 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Annual Review of Oceanography and Marine Biology* **19**:513–605.
- Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Underwood, A. J., and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* **4**:16–20.
- Varley, G. C., G. R. Gradwell, and M. P. Hassell. 1973. *Insect population ecology: an analytical approach*. Blackwell Scientific, Oxford, England.
- Victor, B. C. 1983. Recruitment and population dynamics of a coral reef fish. *Science* **219**:419–420.
- . 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs* **56**:145–160.
- Warner, R. R. 1984. Recent developments in the ecology of tropical reef fishes. *Archiv für Fischereiwissenschaft* **35**:43–53.
- Warner, R. R., and T. P. Hughes. *In press*. The population dynamics of reef fishes. *Proceedings of the Sixth International Coral Reef Symposium*, Townsville.
- Weinberg, J. R., H. Caswell, and J. B. Whitlatch. 1986. Demographic importance of ecological interactions: how much do statistics tell us? *Marine Biology* **93**:305–310.
- Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. *Oikos* **47**:221–222.
- Weldon, C. W., and W. L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology* **61**:23–44.
- Winer, B. J. 1971. *Statistical principles in experimental design*. Second edition. McGraw-Hill, Kogakusha, Tokyo, Japan.
- Wise, D. H. 1975. Food limitation of the spider *Linphya marginata*: experimental field studies. *Ecology* **56**:637–646.
- Yoshioka, P. M. 1982. The role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. *Ecology* **63**:457–468.