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LARVAL SETTLEMENT AND JUVENILE MORTALITY IN A RECRUITMENT-LIMITED CORAL REEF FISH POPULATION[1]

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Abstract. The temporal and spatial patterns of larval settlement of the bluehead wrasse, *Thalassoma bifasciatum,* were documented in the San Blas Islands of Panama. Daily censuses indicated that larvae settle onto coral reefs in brief episodes that tended to occur around the new moon and peak in intensity between August and December of each year. The magnitude of settlement each day was unrelated to changes in the local population size but was found to be significantly correlated with the nightly catch of planktonic reef fish larvae in the waters over the reef. The spatial pattern of settlement was examined on three scales. On a large geographic scale, 24 reefs within 1000 km^2, there was tremendous variability in settlement intensity that was very consistent from one year to the next. The best correlate of recruit density was exposure to the onshore current. It is suggested that some large-scale oceanographic process determines the intensity of settlement of bluehead wrasses on this scale. The densities of adults on these reefs directly reflected the densities of recruits. Counts of daily otolith increments indicated that those larvae that settled onto low-density reefs subsequently grew significantly faster. On an intermediate scale, sites within 1 km^2, there was no consistency among sites or months in settlement intensity, suggesting that variance in settlement intensity on this scale may be the product of random processes. On the smallest scale, habitat selection within a patch reef, it was found that recruits had distinct preferences in their choices of settlement sites.

The daily mortality schedule of bluehead wrasses indicated that mortality was extremely high for the first 3 d on the reef. Juvenile mortality was, furthermore, found to be independent of density. As a result, the patterns of larval settlement of bluehead wrasses persisted into the adult population relatively unchanged. It is therefore proposed that the distribution and abundance of bluehead wrasses in this region are more a product of the external processes controlling larval settlement than of any biological interactions within the reef assemblage.

Key words: Caribbean; coral reef fishes; larvae; mortality; recruitment; settlement; Thalassoma.

INTRODUCTION

Ecologists in search of the mechanisms regulating the sizes of animal populations have traditionally concentrated their efforts on processes occurring within adult populations. For reef fishes, this approach has been singularly unproductive (reviewed in Sale 1980). A major reason for this failure may be that reef ecologists were ignoring the potentially powerful effects of the population dynamics of larval and juvenile fishes. Virtually all of the thousands of species native to coral reefs have a pelagic larval stage that remains in the plankton for a period of weeks or months (Breder and Rosen 1966, Sale 1980). Since coral reefs are patchy habitats and reef fishes are generally sedentary, the only significant recruitment to local reef fish populations comes from the settlement of planktonic larvae. Some marine invertebrate communities that are similarly dependent on planktonic larvae have proved to be governed by settlement processes (e.g., Keough 1984*a*). The extent to which reef fish populations are affected by the patterns of settlement of larvae is as yet an unresolved question.

Although the assumption that animal populations are close to the carrying capacity of their environment is firmly entrenched in population ecology (MacArthur 1972), it is becoming apparent that many reef fish populations are not limited by the supply of resources on the reef. Some recent evidence indicates that a shortage of competent larvae can keep reef fish populations below the levels at which the supply of food and space limits population sizes (Williams 1980, Doherty 1982, 1983*a* for damselfishes and Victor 1983*a* for wrasses). These studies have been performed on species that are both abundant and unspecialized, and thus most likely to have saturated their habitats. The shortage of planktonic larvae certainly does not reflect the production of zygotes by spawning adults, since most reef fishes are prodigiously fecund, often releasing many thousands of eggs over a period of days or weeks (Sale 1980). The ultimate cause of the lack of recruits to the reef population must therefore lie in the planktonic stage.

While it is widely appreciated that a detailed knowledge of the early life history of reef fishes, from the planktonic larval period through settlement and the juvenile stage, is essential to our understanding of reef fish ecology, there is little direct information available on the subject (Helfman 1978, Sale 1980, Anderson et al. 1981, Warner 1984). This is in part a result of the difficulties in studying small and inconspicuous subjects, and in part because of a traditional lack of interest. The recent development of the otolith increment aging technique, which is especially useful for very

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young fishes, has sparked new interest in the early life history of fishes by providing an extremely accurate and precise tool for acquiring information on ages and growth rates of young fishes (Panella 1971, 1980, Brothers et al. 1976, Brothers and McFarland 1981, Victor 1982, 1983*b*, Brothers et al. 1983).

In the first part of this study I describe both the temporal and spatial patterns of larval settlement of the bluehead wrasse, *Thalassoma bifasciatum,* onto coral reefs in the San Blas Islands on the Caribbean coast of Panama. In addition to merely describing these patterns, I attempt to discover whether the determinants of settlement intensity lie within the reef population or in the planktonic realm of water-mass movements and larval densities. Although the first part of this question has begun to be treated experimentally (Williams 1980, Doherty 1983*a*), it is difficult to resolve the entire question by experiment, primarily because oceanographic processes are, by nature, not amenable to experimentation. It is my aim in this study, which is not experimental, to assess the validity of some of the alternative hypotheses that have been proposed to account for the dynamics of settlement in reef fishes, and perhaps identify possible causal mechanisms by a thorough documentation of the patterns of settlement in this species.

In the second part of this study I examine the relationship between the density of juveniles and the daily mortality rate of an undisturbed population of bluehead wrasses. The importance of larval settlement patterns depends upon the degree to which these patterns are maintained in the adult population. The levels of juvenile mortality and, in particular, how these respond to changes in density, directly affect the relationship between settlement patterns and population sizes. If juvenile mortality rates were density-independent, then the observed patterns of settlement would persist into the adult population. If juvenile mortality rates greatly increased with density, then adult population sizes would not directly reflect settlement patterns, but would probably be more stable and responsive to those density-dependent factors influencing both juvenile and adult mortality rates. There is virtually nothing known about natural juvenile mortality rates in coral reef fishes, despite the fact that these rates could potentially determine the dynamics of populations.

Materials and Methods

The bluehead wrasse population on ≈50 coral outcrops was censused daily from 10 June 1981 until 3 January 1983. The study area was on Ukubtupo reef near the island of Porvenir in the western San Blas Islands. These islands form a long archipelago that extends along the Caribbean coast of Panama in Central America. The outcrops were isolated in a shallow seagrass bed and were at least 10 m from any other suitable bluehead wrasse habitat. This kind of habitat is a typical nursery area for young bluehead wrasses in the San Blas Islands, although this species is extremely flexible in its settlement habitat requirements and settles on reefs as well. Adult bluehead wrasses live mainly on the coral reef flat and edges and thus were not resident in the area. Since no new individuals larger than typical new recruits appeared in the study area, it is likely that there was no immigration of settled fish and recruitment was solely by the settlement of planktonic larvae. Juveniles that were approaching maturity (≈30 mm SL and 3 mo of age) emigrated to join the adult population on nearby reefs and were rarely observed to remain within the census area.

Individual residents of each outcrop were distinguished by their size. Recruits grow quickly and it was possible to see the size difference between individuals only a few days apart in age. It was also possible to distinguish first-day fish from those that had been settled for two or more days by behavior; first-day fish stayed much closer to the substrate. Since younger juveniles rarely moved very far from the outcrop on which they first appeared (11.8% of the recruits were recorded moving from their home site in their first month; of these only 1.4% had moved farther than 2 m), I was able to track the movement of individuals and record their date of appearance as well as the date they were last seen. Of the 692 recruits I recorded settling, 47 were collected on the day of their appearance and therefore were included only in settlement rate statistics. For each day of the study I calculated the number of new recruits that settled, the number of resident juveniles that disappeared and their age, and the total number of residents.

An additional 958 juvenile bluehead wrasses were collected from various reefs in the San Blas Islands between November 1980 and January 1983 to augment the data on settlement dates obtained within the census area. Since it has been demonstrated that there are both daily increments and a mark corresponding to settlement on the otoliths of bluehead wrasses, the date of settlement of any individual can be calculated simply by subtracting the number of daily increments between the settlement mark and the edge of the otolith (the age since settlement) from the date of collection (Victor 1982). The otoliths were removed from each of the fish captured and the date of settlement was calculated from daily otolith increment counts following the procedure described in Victor (1982).

In order to test whether the intensity of settlement of bluehead wrasse larvae within the census area simply reflected the availability of planktonic larvae, I estimated the abundance and diversity of planktonic fish larvae in the waters passing over the reef by sampling at a night-light. The larval fish were attracted to a light placed ≈0.25 m above the surface of the water directly over the study site, where the water depth was ≈1 m. An aquarium dipnet, ≈12 × 8 cm with 2 mm mesh, was swirled through the surface waters beneath the light and periodically raised and the contents emptied into

a container. I found that fish larvae were not attracted to the light when the moon was out, so all night-light samples were taken either before the moon rose or after it had set. For most of the lunar month I night-lighted in the late evening, several hours after sunset, but during the week before the full moon, when the moon set progressively later in the night, the sampling was performed an hour or so after moonset. Samples were not taken between a few days before full moon and a few days after full moon, because during this time the moon set just before dawn or rose just after sunset, leaving no extended period of dark.

The night-lighting was conducted for the entire duration of the settlement monitoring study. Between 5 June 1981 and 20 October 1981, the sampling was done for 2 h each night. Between 21 October 1981 and 6 September 1982, the sampling period was reduced to 1 h. The sampling period was further reduced to a half-hour each night from 7 September 1982 until 3 January 1983. The fish larvae captured were preserved in 95% ethanol and later sorted, identified, and counted. In addition to sampling by night-lighting, I towed a plankton net immediately after performing the night-lighting on a number of nights in order to compare the two plankton sampling techniques. The plankton net was conical, 0.75 m wide at the mouth, with 1-mm mesh, and was equipped with a flow meter. The tows were conducted in an area of lagoon ≈ 15 m in depth located less than a kilometre generally upcurrent of the study area.

The spatial pattern of settlement was examined on three very different size scales. The largest scale included 24 reefs within an area of ≈ 1000 km^2 in the western end of the San Blas Islands. The density of juvenile bluehead wrasses was measured on each of the 24 reefs in August 1981 and again in January 1983. The surveys were done in qualitatively similar habitats (shallow reef flat) and at the same depth (≈ 1 m) on each reef. Densities were measured by slowly swimming along a 10-m transect, counting the numbers of fish within a metre of the line. From 5 to 20 of these 20-m^2 transects were censused at each site visited. On the second visit, the density of adults associated with each reef was determined as well. The numbers of adults were counted along equal numbers of transect lines parallel and perpendicular to the edge of the reef facing the current. In this way some transects passed through the feeding schools that concentrate at the upcurrent ends of the reef, while others covered the reef flat. Since adults are not uniformly distributed over the reef, these density estimates are more useful for comparisons between reefs rather than for absolute measures of overall density.

The daily increment aging method permits comparisons of growth rates of bluehead wrasses that settle in different places. Although growth rate is only one of many factors affecting fitness, for this one measure, at least, it is possible to determine whether recruits are selecting settlement sites on the basis of habitat quality. For this comparison, all of the juveniles encountered within the transects were collected in August 1981, except at sites with high densities where the juveniles from only a fraction of the transects were collected. In January 1983, large samples of adults were collected at two sites: Naibetupo, a site characterized by very low densities of recruits, and Chichime, the site with the highest density of recruits. I measured each fish and estimated age since settlement by counting the number of daily increments between the settlement mark and the edge of the otolith (Victor 1982).

I estimated the variability in settlement intensity on a smaller spatial scale by counting the number of new recruits on four delineated areas of reef (within 1 km^2) near the island of Porvenir in the westernmost San Blas Islands. These sites were visited regularly each month for 5 mo in mid-1981. Visits were made during the full moon when larval settlement had usually ceased. Only those recruits that had settled during the previous new moon (recognized by their size and validated by otolith increment counts) were recorded.

In addition to these geographical patterns of settlement intensity, I recorded details of microhabitat selection by settling bluehead wrasses. I selected a single patch reef of ≈ 1000 m^2 (Snapper reef, ≈ 2 km north of Wichubhuala), and removed new recruits (usually within a week of settlement), recording (1) what substrate comprised the majority of their home range (usually a fraction of a square metre; the complex topography and biota precluded finer assessments of substrates), (2) their depth, and (3) their position on the reef. Between July and October of 1981, 215 bluehead wrasse recruits were removed. The proportions of substrates were measured by running transects across the reef 5 m apart and recording the substrate at points 1 m apart along the transect lines. The reef was mapped in detail, recording depth contours and the locations of prominent coral heads. The proportion of reef area at different depths was then determined with a planimeter from the map. Settlement site preferences were analyzed with the chi-square statistic.

Results

Temporal patterns of settlement

The daily censuses of bluehead wrasse juveniles revealed that recruits of this species appeared in brief and sporadic episodes throughout much of the year (Fig. 1, bottom). It is often assumed that the appearance of new recruits on a particular day is indicative of settlement that day or the previous night (e.g., Williams and Sale 1981, Sale et al. 1984). This assumption may not hold for all reef fishes, since it has been experimentally demonstrated that larvae of another Caribbean wrasse, *Halichoeres bivittatus,* spend ≈ 5 d buried in the sand metamorphosing before appearing on the reef (Victor 1983*b*). This period of hiding results in the

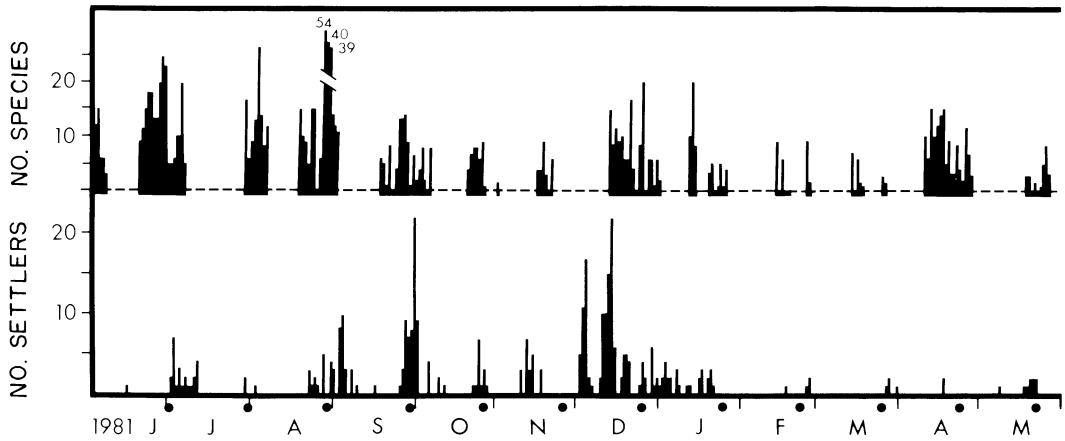

FIG. 1. The daily pattern of planktonic larval diversity (upper) as measured by the number of species of reef fish larvae captured at a night-light, compared with the daily pattern of bluehead wrasse recruitment onto a number of isolated coral outcrops (lower) over a period of 18 mo in the San Blas Islands. Dashed baselines in the upper histogram indicate days when night-lighting was not performed. ● = new moon.

formation of a conspicuous band of about five faint increments on the otolith. Since bluehead wrasse juveniles have an identical band that is absent on the otoliths of planktonic larvae (Victor 1982) but present in its entirety at the edge of otoliths of newly appeared recruits, it is likely that bluehead wrasses also spend ≈5 d in hiding before appearing on the reef. I therefore use the date of appearance minus five an an estimate of the date of settlement of recruits recorded in censuses. This is not an issue for estimates of the date of settlement calculated from otoliths of juveniles, since the five daily increments within the settlement band were counted as postsettlement increments.

There was some lunar periodicity to the pattern of settlement. Settlements of bluehead wrasse larvae tended to occur during the 2 wk around the new moon (Fig. 2). Settlement was not randomly distributed among the 4 wk of the lunar month (chi-square test, $P < .0001$). Settlement was particularly low during the week around the full moon, when only 9.6% of the fish sampled had settled. In contrast, 44.8% of the fish sampled had settled during the week around new moon. The second mode of the peak in Fig. 2 is primarily the product of one exceptionally large episode of settlement recorded in 1980 that occurred a few days after the new moon (Victor 1983*a*).

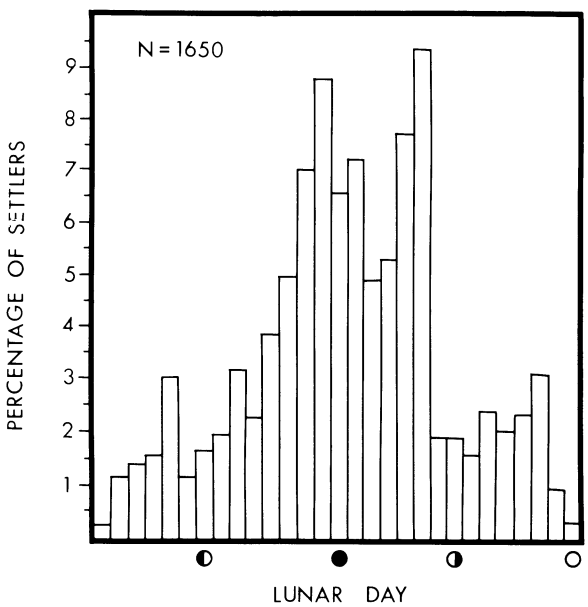

FIG. 2. Frequency distribution of larval settlement by lunar day. ● = new moon, ○ = full moon.

Occasional censuses in the study area were conducted for 2 yr after the daily monitoring period had ceased. Settlement appeared to be consistently low from January to June, a period corresponding to the dry season and the beginning of the wet season in Panama (Glynn 1972). As a result of the sharp reduction in recruitment, the population size of juvenile bluehead wrasses within the census area decreased steadily through much of the dry season, reaching a low close to zero by April and May of each year (Fig. 3).

Temporal correlates of settlement intensity

Settlement rates did not respond to natural decreases in the resident bluehead wrasse population. Daily appearances of new recruits in the census area had no significant correlation with the number of juveniles disappearing on either the day before appearance, the day of settlement, or any day up to 10 d before the day of appearance (Fig. 4). There was a very significant positive correlation between the number of recruits appearing and the total population size on any day up to 2 wk before the day of appearance ($P < .0001$). Since settlement occurred in episodes lasting for many days and certain seasons had higher settlement rates than others, a positive correlation between settlement and the number of settled fish would be expected.

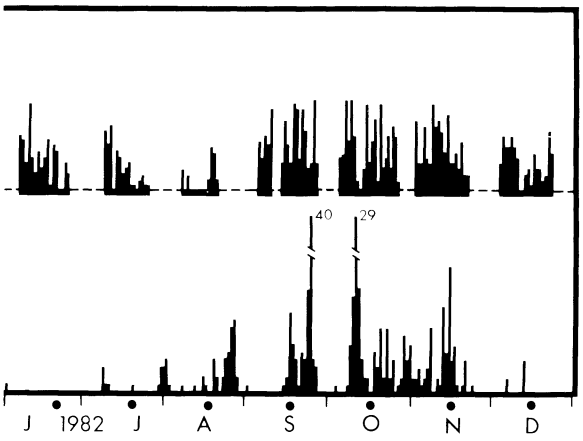

FIG. 1. Continued.

I estimated the availability of bluehead wrasse larvae in the plankton by capturing reef fish larvae attracted to a light at night. Reef fish larvae apparently settle during the night. About 93% of the fish larvae recorded settling onto an experimental reef in the San Blas Islands settled between dusk and the following dawn (D. R. Robertson and B. C. Victor, *personal observation*). There was a significant correlation between the number of species of fish larvae captured at a night-light and the number of fish larvae captured in plankton tows during the same night, the traditional method for determining the density of planktonic fish larvae ($P < .0001$) (Fig. 5). Since plankton tows characteristically yield very few coral reef fish larvae, they were not used for daily estimates of larval fish availability.

Bluehead wrasse larvae themselves were almost never captured in either night-light samples or plankton tows. While this fact provides some assurance that sampling at the census site did not reduce the number of potential recruits, it does necessitate an indirect method of assaying bluehead wrasse larval densities. I found that the only possible way to estimate their abundance was to assay the abundance of all reef fish larvae and assume a positive correlation. I used the number of species of larvae captured at the night-light rather than the number of individuals because of the occasional appearance of very large numbers of a single species.

Despite the potential masking of a real relationship between larval abundance and settlement intensity by the use of an indirect estimate of bluehead wrasse larval abundance, I discovered a strong correlation between the number of species of fish larvae captured at the night-light and the number of bluehead wrasse juveniles that appeared on the reef 5 d later ($P < .0001$) (Fig. 4). Despite the level of significance, the relationship is not particularly tight (a correlation coefficient of 0.27), since high densities of many reef fish larvae would often occur without a concomitant increase in the settlement of this single species. Nevertheless, the pattern of appearances usually reflected the pattern of larval abundance of 5 d before (especially June to September 1981 and September to November 1982, Fig. 1). The existence of a highly significant relationship suggests that (1) bluehead wrasse larval densities are positively correlated with those of other species of reef fish, and (2) the intensity of settlement reflects the availability of larvae in the water passing over the reef.

Spatial patterns of settlement

On the large geographic scale, the densities of bluehead wrasse juveniles varied tremendously. The densities of juveniles within the San Blas Islands ranged over three orders of magnitude. In January 1983, juvenile densities ranged from zero on several reefs in the study area to a high of close to 1 juvenile/m^2 on Chichime reef (Fig. 6). These patterns were persistent over time; the densities of juveniles in January 1983 were significantly correlated with the densities on the same reefs recorded in August 1981 (Spearman cor-

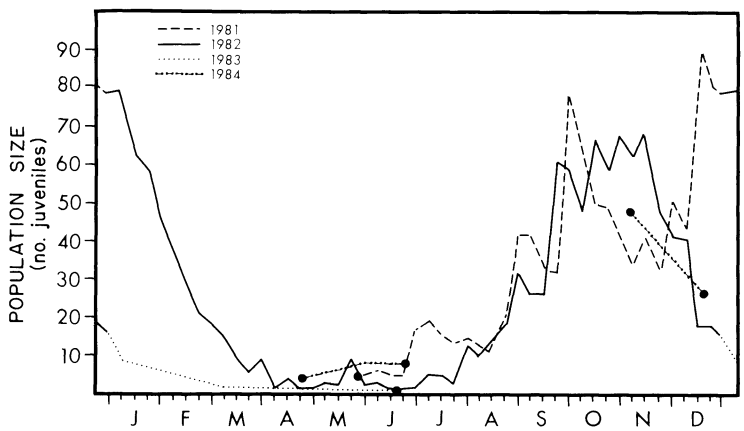

FIG. 3. The annual cycle in the total size of the juvenile population within the daily census area on Ukubtupo Reef.

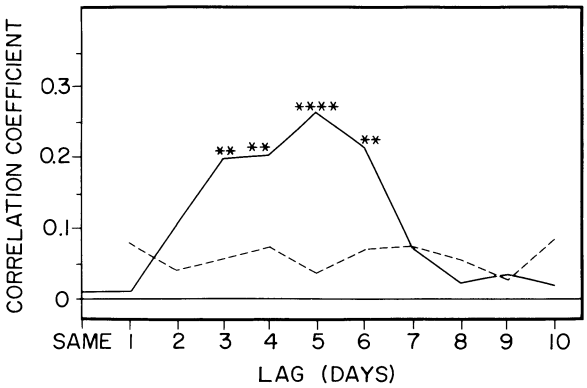

FIG. 4. Correlates of the number of bluehead wrasse recruits appearing per day. -- the correlation coefficients between the number of bluehead wrasse appearing on the reef and the number of resident juveniles disappearing on the same day and on each day up to 10 d before the day of the appearances. —— the correlation coefficients between the number of bluehead wrasse appearing on the reef (Fig. 1, lower) and the number of larval species at the night-light (Fig. 1, upper) on the same day and on each day up to 10 d before the day of the appearances (lagged serial correlations). •• = $P < .01$, •••• = $P < .0001$.

relation coefficient of 0.96, $P < .0001$), although the August 1981 densities were consistently lower because of seasonal fluctuations in larval settlement.

On a smaller scale, within 1 km^2, there was no apparent consistency in the settlement intensity among sites within each month (Fig. 7). In fact, each site had its maximal settlement on a different month, and the ranking of months by settlement intensity changed from site to site. A two-way ANOVA without replicates was used to analyze the numbers of recruits settling onto the four sites on the six different months. Neither site nor month had any significant effect on the number of individuals settling per month ($P > .1$ and $P > .4$, respectively).

Spatial correlates of settlement intensity

High densities of adults did not inhibit the settlement of larvae. On the contrary, the density of juveniles at any particular site directly reflected the density of adults at that site, even at the highest densities (Fig. 8, Spearman correlation coefficient of 0.97, $P < .0001$). Low densities of juveniles and adults at a site were not necessarily indicators of the unsuitability of the site for bluehead wrasses, since both juveniles and adults in low-density sites had significantly higher growth rates than those in high-density sites (Table 1). Because the size distribution of individuals was neither uniform nor consistent between sites, a simple comparison of the age-growth curves was not possible. Instead, I removed the effect of size by selecting narrowly restricted size cohorts of both juveniles and adults that had sufficiently large sample sizes to compare the mean ages of each cohort on low- and high-density reefs.

The distinct geographical pattern of settlement intensity suggests that a large-scale process may be controlling the intensity of settlement in this area (Fig. 6). When various simple geographic correlates of settlement intensity are evaluated, proximity to the onshore current is the factor most closely correlated with the settlement intensity between sites (Spearman correlation coefficient of 0.86, $P < .0001$). Apparently, the first reefs encountered by the onshore current tended to have higher settlement of bluehead wrasse larvae. Other measures, such as the distance from river outflows, longitude, the distance from the mainland, and the distance from the nearest other reef, accounted for far less of the variance (Spearman correlation coefficients of 0.45, 0.45, 0.23, 0.19, and $P < .03$, .03, .28, .38, respectively).

Microhabitat selection

Newly settled bluehead wrasses did not choose settlement sites at random (Table 2). Sand, sponges, and anemones were avoided by new recruits, while dead coral surfaces were strongly favored. No preference for or against live corals was evident. Significant preferences were found within the categories of dead and live corals. Recruits strongly preferred dead coral surfaces that were predominantly flat or nonbranched (*Acropora palmata* and *Montipora* spp.). However, among living coral substrates, only the branching fire coral, *Millepora,* was favored. Since juvenile bluehead wrasses take refuge in holes and crevices within dead corals, it is likely that this latter preference was a result of the availability of dead surfaces below the living matrix of this coral, and perhaps because of the protection afforded by the powerful nematocysts from which the common name of this coral is derived. Bluehead wrasse recruits strongly preferred shallow reef substrates as well. Over 86% of the individuals had settled in waters shallower than 2 m, although these areas were esti-

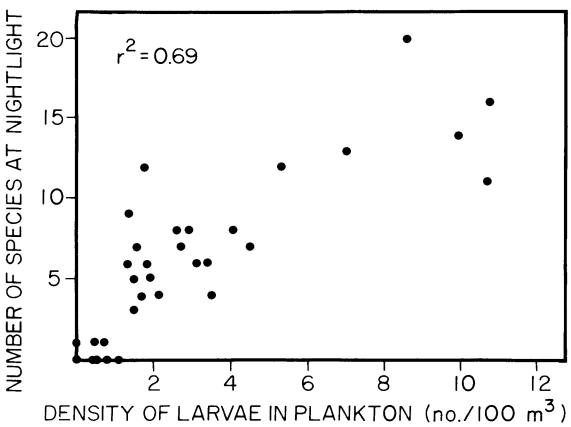

FIG. 5. Relationship between the number of reef fish larval species captured at a night-light and the density of reef fish larvae in the plankton (measured with plankton tows) on the same night.

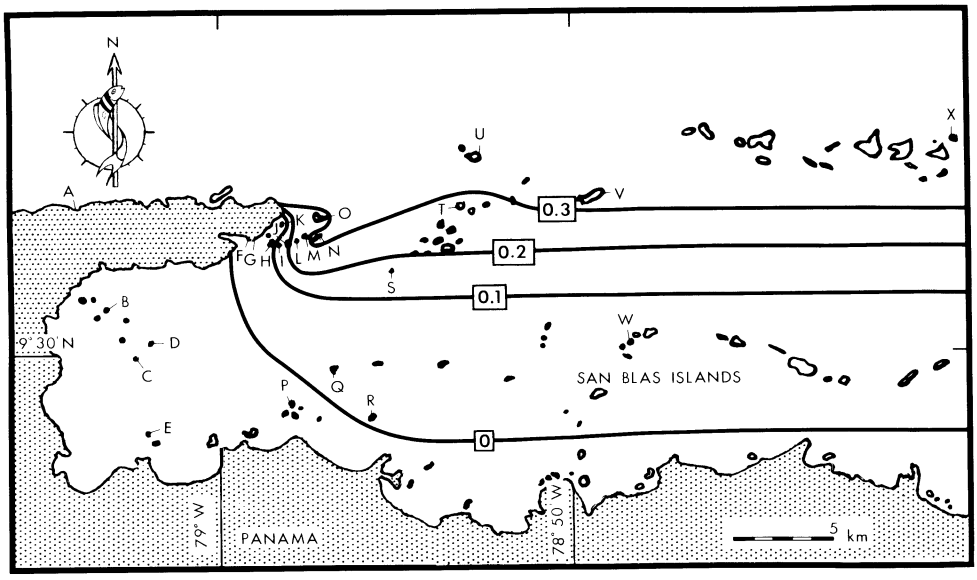

FIG. 6. Map of the San Blas Islands of Panama showing isopleths of juvenile densities (number per square metre) recorded in January 1983. The prevailing current recorded over several years at a reef near site L was from 1° west of due north. A: Puerto Geladi, B: Mandinga, C: Bajo Tridente, D: Mandinga, E: Mandinga, F: Ulugsukun, G: Mackerel, H: Guigalatupo, I: Korbiskie, J: Taintupo, K: Punta San Blas, L: Ukubtupo, M: Wichubhuala, N: Aguadargana, O: Porvenir, P: Carti, Q: Achuertupo, R: Naibetupo, S: Cayo Gallo, T: Helmet, U: Chichime, V: Masargantupo, W: Salar, X: Holandes.

mated to be at most only 39.3% of the total reef surface area.

Juvenile mortality

The mortality rate of juvenile bluehead wrasses in the daily census area on Ukubtupo Reef was relatively high during the 1st wk after their appearance on the reef (Fig. 9). Of the 645 juveniles recorded settling, 11.6% disappeared within a day of their first appearance, and a further 10.4% disappeared within the next 2 d. The mortality rate then dropped to ≈3%/d on day 4 and then showed a gradual downward trend. After 3 wk, mortality had fallen to ~1%/d, and subsequently the rate of disappearance remained uniformly low. As juveniles became older, however, emigration rather than mortality probably began to account for an increasing proportion of the disappearance rate.

Since there are seasonal peaks of settlement of larvae, the age and density of juveniles within the census area automatically covary. When there were large numbers of juveniles, they tended to be young. It is therefore difficult to distinguish whether high mortality rates are entirely due to the youth of the population or are a function of high density. Without experimental manipulations, an efficient method to tease apart the effects of these two important factors on mortality rates would be to compare mortality rates for each daily age class over a range of densities. One would need extremely large numbers of juveniles for such an analysis, which would preclude accurate daily monitoring. In view of these limitations, I partially removed the effect of age by combining age classes that appeared to suffer similar mortality rates, and then tested for the effect of density within those age classes. I divided the sample into two age classes, the 1–3 d age class and the 4–34 d age class. Mortality rates within these two classes are relatively consistent (Fig. 9), although even within these classes there was increased mortality in younger fish. It should be emphasized that this deviation is in a conservative direction for a test of density-independence of mortality rates (i.e., more likely to show density dependence even if mortality was independent of density). The lack of independence of the population sizes each day is similarly conservative, since any resulting autocorrelation would also make it more likely to find density dependence.

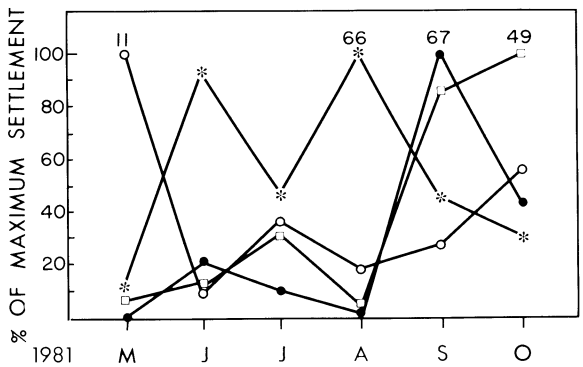

FIG. 7. Variability in settlement among four sites within 1 km² over 6 mo. □ Ukubtupo, ○ Vieja reef, ● Aguadargana, * Snapper reef. The numbers at each maximum represent the number of recruits on the maximum settlement month for each site.

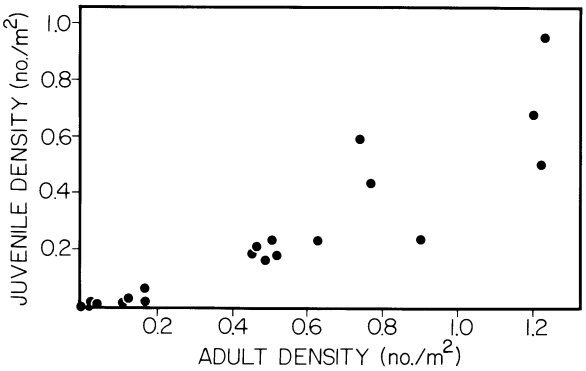

FIG. 8. Relationship between adult bluehead wrasse density and juvenile density recorded in January 1983 on 24 reefs in the San Blas Islands of Panama. Four reefs are represented at the origin.

For each of the two age classes an analysis of variance was performed to determine the effect of the total juvenile population size on the proportion of the selected age class disappearing each day. At low population densities the proportion disappearing per day was calculated from far fewer individuals than on days when populations were high, so some weighted lumping of days was necessary. This was achieved by ranking the daily measures of the proportion disappearing per day by population size, and then dividing the sample into groups of days containing equal fish-days. For example, one daily measure of proportion disappearing with a population of 100 fish would rank as equal to 50 daily measures with a population of only two individuals. In this way, groups represented equivalent "exposures" of individuals to mortality. For each of the two age classes, the mean population size and the mean of the arcsine-transformed proportion disappearing were then used in a one-way analysis of variance.

The daily mortality rates for the 1–3 d age class were divided into 24 groups representing mean population sizes ranging from 2.1 to 90.0 individuals, while the mortality rates for the 4–34 d age class were divided into 38 groups representing mean population sizes ranging from 1.3 to 86.0 individuals (each group comprised ≈ 300 fish-days, a grouping large enough to expect an average of 10 deaths). The results of the analysis of variance indicated that there was no significant effect of density on the mortality rate of juveniles in either the 1–3 d age class ($P > .28$) or the 4–34 d age class ($P > .06$). There were, furthermore, no significant differences between the mortality rates of the quarter of the groups at lowest densities and the quarter at the highest densities for either age class (t test on arcsine-transformed proportion disappearing, for 1–3 d age class $P > .64$, for 4–34 d age class $P > .40$). Since there is still an association between density and age within these two age classes (that could lead to a finding of significance due to age effects alone), the lack of more significant effects of density in this analysis indicates that mortality rates within this population are mostly independent of density.

DISCUSSION

A scarcity of data has not deterred the growing consensus that the larval ecology of reef fishes may be the key to a heretofore elusive understanding of what is controlling the abundance and distribution of reef fish populations. It is still an open question whether patterns of settlement reflect processes occurring within the reef population or processes taking place in the oceanic plankton. This is an important distinction, for if oceanographic processes can account for the observed patterns of both juvenile and adult abundances, one would not expect traditional equilibrial or other resource-limitation-based ecological theories to apply to this particular system.

Temporal pattern of settlement

One of the first discoveries about coral reef fish settlement was that the intensity of settlement is notably variable over time. Pronounced seasonal patterns of settlement have been found to occur at One Tree Island on the Great Barrier Reef (23°30′ S) where virtually all settlement occurs during the austral summer (Russell et al. 1974, 1977, Talbot et al. 1978, Williams 1983). In more tropical areas the seasonality of settlement is less distinct. Settlement in the tropical Caribbean is reported to be high in the northern spring and fall and low in the winter (Luckhurst and Luckhurst 1977, McFarland et al. 1985). Bluehead wrasse settlement on the Caribbean coast of Panama (latitude 9°30′ N) tends

TABLE 1. The age in days of bluehead wrasses within four size (standard length) cohorts from high and low density reefs in the San Blas Islands of Panama.

	Size cohort (mm)											
	18–20			38–41			49–52			60–63		
	n	Mean SL (mm)	Mean age (d)	n	Mean SL (mm)	Mean age (d)	n	Mean SL (mm)	Mean age (d)	n	Mean SL (mm)	Mean age (d)
High density	14	18.8	39.3	9	39.0	169.9	9	50.3	229.2	8	61.1	375.5
		NS	**		NS	**		NS	****		NS	****
Low density	8	19.5	34.5	9	39.9	128.4	9	50.7	170.4	8	61.4	214.0

** $P < .01$, **** $P < .0001$ (t tests of the differences of means).

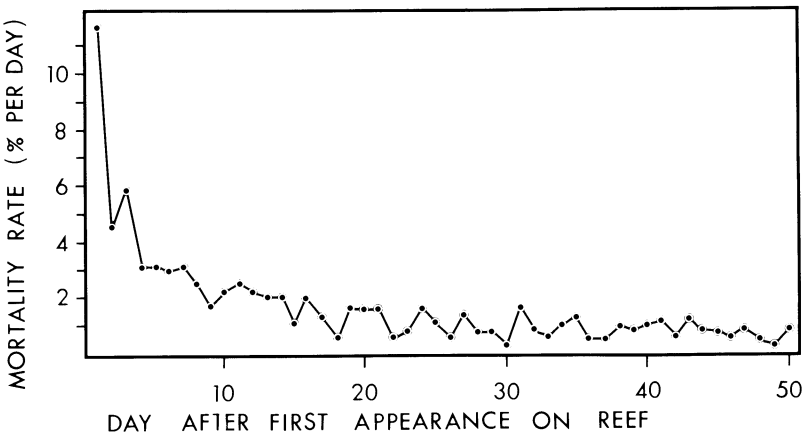

FIG. 9. Daily mortality rates of juvenile bluehead wrasses within the daily census area on Ukubtupo Reef. Mortality rate is defined as the percent of a settling cohort disappearing each day.

to peak in the late summer and fall and is very low in the winter (dry season). No spring peak was evident from the juvenile abundance cycles recorded between 1981 and 1984.

One explanation for seasonal cycles of settlement in tropical reef fishes is that settlement cycles simply reflect the varying breeding capabilities of adults. For example, seasonal energy surpluses could lead to higher fecundities. The usual assumption, however, is that the observed seasonality of settlement reflects seasonal variation in larval survival rates (Luckhurst and Luckhurst 1977), and, furthermore, that adult spawning cycles are tailored to these predictable variations (Watson and Leis 1974, Johannes 1978, Doherty 1983*b*). In subtropical areas where the relationship between spawning and settlement seasons is strong (Doherty 1983*b*) it is particularly difficult to separate cause from effect.

In areas closer to the equator, such as Panama, the less intense seasonality permits some evaluation of the relative importance of these two alternatives. Since bluehead wrasses in Panama spawn every day throughout the year (Robertson and Hoffman 1977, Warner and Robertson 1978), the observed seasonal cycles of settlement probably reflect seasonal variation in the survival rates of their planktonic larvae. I would hasten to emphasize that without thorough documentation of the proportion of the population spawning each day, the fecundity of the spawners, the actual size of the population, and how these vary over the range of the species, the degree to which settlement periodicity is influenced by variability in egg production must remain unknown. Bluehead wrasses may persist in spawning during periods which will probably result in relatively low settlement success because of (1) the inherent unpredictability of larval success rates at any specific time, a product of an extremely variable larval life, from 38 to 78 d for this species (Victor 1986), combined with the occasional successful settlement during the dry season, and (2) the relatively high mortality rates of adults of this species (13.5%/mo, Victor 1983*a*), which would reduce the advantages of postponing reproductive effort until the optimal season for larval survival.

The dry season in the San Blas Islands of Panama is characterized by very low precipitation, increased turbulence, strong and continuous trade winds, and a consistent current from the north (Glynn 1972). Low survival of planktonic larvae during this period could be a result of the breakdown of concentrated food patches becaue of turbulence, as suggested by Doherty (1983*b*). Alternatively, zygotes could be swept far away

TABLE 2. Chi-square analysis of the habitat preferences of bluehead wrasse recruits on a patch reef in the San Blas Islands.

Habitat type	Number of recruits: Expected	Number of recruits: Observed	Chi-square
Sand	21	0	
Sponge	11	1	
Colonial anemone	14	0	
Dead coral	112	155	
Live coral	57	59	
			61****
Dead *Millepora* spp.	30	8	
Dead *Acropora palmata*	95	95	
Dead *Montipora* spp.	10	27	
Dead *Agaricia* spp.	20	25	
			46****
Live *Millepora* spp.	30	44	
Live *Acropora palmata*	7	0	
Live *Montipora* spp.	4	1	
Live *Agaricia* spp.	18	14	
			17****
0–2 m	85	185	
2–4 m	21	20	
>4 m	110	10	
			209****

**** $P < .0001$.

from the coast and the return of competent larvae prevented by the continuous net movement of water in one direction (Johannes 1978). The fact that some species of reef fishes do have some of their peak settlements during the dry season (D. R. Robertson, *personal communication*; B. C. Victor, *personal observation*) argues that the obstacles to bluehead wrasse settlement during this period do not affect all reef fish species.

There is much less information available on daily variability in settlement of reef fishes. Major daily fluctuations in numbers of new recruits have been reported to occur both on lunar cycles (Randall 1961, McFarland et al. 1985) as well as independent of lunar cycles (Williams 1983), and are generally ascribed to similar patterns of spawning by adults. In contrast, the bluehead wrasses observed in the San Blas Islands settle in brief and sporadic episodes loosely associated with the new moon, but appear to spawn daily without a lunar pattern. It is therefore likely that the observed daily settlement pattern reflects the fluctuating survival rates of larvae, rather than the variable production of zygotes. The caveat mentioned above applies, however; until the source population of larval recruits is known, the relevance of local spawning patterns to local settlement patterns remains uncertain.

Larval movement inshore around the time of the new moon would ensure that larvae pass over reefs on the darkest nights of the month, since the approach of the new moon in the lunar cycle means that the moon is both waning and visible for a shorter period each night. Tides may also play a role in promoting settlement at the time of the new moon, since the spring tides (periods with the greatest tidal flux) occur near the new and full moons. If larvae rely on tidal currents to move them inshore, or actively migrate into onshore currents, greater tidal fluxes would result in larger inshore migrations. The tendency to settle near the time of the new moon may thus be primarily an adaptation to reduce visual predation on incoming fish larvae by nocturnal planktivores, since tidal movements, usually invoked as the causal factor in lunar cycling of settlement (Johannes 1978), should generally be no greater on new moon nights than on full moon nights. The degree of unpredictability of bluehead wrasse settlement observed in this study clearly indicates that other, perhaps stochastic, factors also have an important effect on the exact timing of settlement pulses.

Although larval settlement has been demonstrated to occur on seasonal and lunar cycles, a more important question for many reef ecologists is what determines the magnitude of settlement. Perhaps the only point upon which all studies of reef fish settlement have agreed is that the magnitude of settlement is extremely variable over time (Luckhurst and Luckhurst 1977, Russell et al. 1977, Molles 1978, Talbot et al. 1978, Williams and Sale 1981, Victor 1982, 1983*a*, 1984, Williams 1983, Sale et al. 1984, McFarland et al. 1985, Shulman, *in press*). In direct contrast to this general consensus, one of the more contested subjects in reef fish ecology is what exactly determines this magnitude. Traditional ecological theory emphasizes density-dependent processes (see Anderson et al. 1981). This has led some coral reef fish ecologists to presume that the specializations they have observed among reef fishes are indicative of severe competition for limited resources, and thus fish populations must be regulated by density-dependent factors (Smith and Tyler 1973, Smith 1978, Anderson et al. 1981). A different hypothesis, proposed by Sale (1978), included the supposition that space on the reef is limited and that individuals settle from a pool of superabundant larvae when spaces were opened up by the death of residents (the lottery hypothesis). Both hypotheses require that the magnitude of larval settlement directly reflect decreases in the size of the resident population.

Recent evidence does not support either view (Williams 1980, Robertson et al. 1981, Doherty 1982, 1983*a*, Victor 1983*a*, 1984). The number of damselfish recruits settling onto Australian coral reefs has been shown to be independent of the size of the local damselfish populations. In these experiments, the removal of all resident damselfishes on small patch reefs did not affect the number of damselfish recruits appearing on the reefs after the manipulation (Williams 1980, Doherty 1983*a*). My results demonstrate that the number of bluehead wrasse larvae recorded settling each day into the study area not only bore no relation to the number of juveniles that had recently disappeared, but furthermore, was positively correlated with the number of living resident juveniles. The positive correlation was produced because settlement peaks of this species occur over a number of days and in certain seasons, such that high rates of settlement usually occurred just when resident juvenile populations had recently increased. Adult bluehead wrasses do not usually occupy the same microhabitat as juveniles and therefore probably have no effect on larval settlement rates. In any case, Victor (1983*a*) found no relation between settlement rates and changes in the size of the adult population of bluehead wrasses on a large Caribbean patch reef.

If the observed rate of larval settlement is independent of changes in the resident population of a species, then settlement rates may simply be a product of the distribution and abundance of mature larvae in the plankton passing over the reef (Williams 1980, Doherty 1982, 1983*a*, Victor 1983*a*). However, observed settlement rates could also be a product of predator densities (Shulman et al. 1983, Shulman 1985*a*), physical disturbances, or competition between taxa (Shulman et al. 1983, Shulman 1985*b*). It is therefore especially important to demonstrate the direct connection between larval abundance in the plankton and intensity of settlement onto the reef. The intensity of settlement of bluehead wrasse larvae onto my study site each day

was significantly correlated with the diversity of larval fish species sampled at a night-light over the study site during the previous night. While my procedure was somewhat indirect, my results indicate that the availability of planktonic larvae in the waters passing over the reef each night probably determines the number of recruits to the reef population.

Spatial pattern of settlement

The intensity of settlement of bluehead wrasse larvae in the San Blas Islands was tremendously variable on a large geographic scale. The pattern of recruit densities among reefs, however, was very consistent from one year to the next, in contrast to both the variability I found on a smaller scale and the variability reported in previous studies. Sale et al. (1984) and Eckert (1984) found that juvenile abundances among a 70-km series of Australian reefs were different and the rank order changed significantly between years. Although it was not suggested by the data, they postulated that there still must be some consistent differences in the attractiveness of different reefs to fish larvae to account for the consistent geographic clines of adult fish abundances on the Great Barrier Reef (Anderson et al. 1981, Williams and Hatcher 1983). The consistency of bluehead wrasse settlement patterns supports the hypothesis that some nonrandom process is controlling the relative intensity of larval settlement on a large geographic scale.

The density of adults was directly correlated with the density of recruits, indicating that the presence of adults does not have the negative effect on the rate of recruitment that would be expected in a lottery or equilibrial system. The best predictor of the density of recruits (and adults) on reefs in the San Blas Islands turned out to be the degree of exposure to the onshore current. Since qualitative observations on the 24 reefs visited indicated that the highly preferred settlement substrate (shallow dead coral surfaces) was by far the most common substrate, comprising the majority of the surface area on each reef, it is unlikely that the availability of suitable settlement substrate accounted for the massive differences in recruit abundance. These results lead one to question whether the spatial variability in settlement of this species is a product of active selection by larvae or merely the product of differing rates of passive delivery.

If the large-scale pattern of settlement reflects an active, and presumably adaptive, choice, one might expect that reefs that are the most preferred (have the highest density of recruits) would be the reefs that have the highest growth rates for both juveniles and adults and the lowest mortality rates. The analysis of the age and growth of bluehead wrasses on reefs with very different recruit densities indicated that, rather than selecting reefs characterized by high growth rates, bluehead wrasse larvae settled primarily on reefs that conferred low growth rates on their residents. The lower growth rates may be a direct product of the high density of wrasses. Those larvae that managed to settle on the low-density inshore reefs had a significantly higher growth rate both as juveniles and adults.

The importance of exposure to the onshore current combined with the possible absence of optimal settlement choices by the vast majority of individuals (on this large geographic scale) suggests that it is unlikely that bluehead wrasse larvae are making active choices among reefs. Reef fish larvae of species with pelagic eggs (such as wrasses) are mainly found in waters some distance from the shore (Leis and Miller 1976, Leis 1982). Given the likelihood that the source of competent larvae is in offshore waters and that the number of recruits reflects the number of competent larvae in the waters passing over the reef, these results support the hypothesis that the density of bluehead wrasse larvae in the plankton is somehow attenuated as offshore waters move inshore over an archipelago of reefs, and that this process accounts for the large differences in recruit densities found within this region.

Some possible mechanisms that would yield such a pattern are: (1) bluehead wrasse larvae settling on the first reef they encounter, or (2) predation on planktonic larvae is very high in inshore waters, or (3) offshore waters do not often penetrate far into the archipelago. These possibilities cannot be evaluated without more detailed information on the behavior of reef fish larvae and the movement of waters between and around reefs. Whether the process of moving inshore is purely passive or the result of active migrations also cannot be answered from the data. Recent findings on the distribution of various species of reef fish larvae off the Great Barrier Reef by Leis and Goldman (1984) indicate that reef fish larvae do not behave simply as passively dispersed particles.

On a small geographic scale (sites within 1 km^2) I found that the spatial patterns of settlement were not consistent over time. The rankings of months by settlement intensity changed from site to site. Settlements of reef fishes onto grids of coral colonies over a similar-sized area on the Great Barrier Reef were also found to be different from each other and not consistent over time (Williams and Sale 1981). These findings (on this scale) agree with the hypothesis proposed by Sale et al. (1984) that fluctuations in settlement intensity may be random, although some predictable fluctuations in current direction or speed (or some other oceanographic process) may ultimately account for all of the seemingly random patterns observed. Since bluehead wrasse larvae have been found to move inshore in a very large patch (>46 km wide), these smaller scale variations are probably a product of heterogeneous distributions of larvae within the large patch (Victor 1984). It is not known whether this heterogeneity is characteristic of planktonic patches of reef fish larvae or is produced by the differential onshore movement of sections of the patch (or front).

The distribution of juveniles on a single reef is often ascribed to habitat selection by settling larvae. While there have been a number of anecdotal descriptions of habitat selection by juvenile coral reef fishes, rigorous analyses of habitat selection by new recruits have only begun to be performed (Sale et al. 1984). I found that bluehead wrasse recruits preferred flat, dead coral surfaces, especially massive corals and elkhorn corals, and completely avoided sand, seagrass, colonial anemones, and sponges. Shallower areas of the reef (<2 m deep) were also preferred over deeper areas. Bluehead wrasse juveniles are generally catholic in their settlement site preferences and commonly settle on any shallow nonliving hard surface. I have even found new recruits that have settled onto submerged cardboard boxes. This lack of specificity may well be characteristic of most coral reef fishes (Sale et al. 1984).

Juvenile mortality

Of all of the factors that could play a role in limiting adult populations of reef fishes, the level of juvenile mortality has received the least attention. While there have been experimental studies on the mortality rates of transplanted fishes (Doherty 1982, 1983*a*), there has been virtually no information published on the levels of juvenile mortality in undisturbed populations other than the report by Doherty (1982) that older juveniles of two Australian damselfishes disappeared at an average daily rate of 0.10 and 0.15%/d. My analysis of the daily schedule of mortality indicates that bluehead wrasse juveniles suffer an extremely high mortality rate for the first few days after their appearance on the reef (22% mortality in the first 3 d), after which their mortality rate declines abruptly. Mortality among adult bluehead wrasses averages 13.5% of the adult population per month (Victor 1983*a*).

Most mortality studies in the field have a suite of problems that are particularly difficult to circumvent. One is that any manipulations that might make censusing easier could have major artificial effects on mortality rates. Transplanting, tagging, or capturing fishes may increase mortality rates from trauma, stress, or predation (and losses from unnatural emigration). Building artificial reefs or restructuring reefs can alter natural predator populations. Another complication is separating the losses from emigration and mortality. In this study, emigration certainly could have accounted for some of the losses, especially among older juveniles. However, since young juveniles rarely moved far from the outcrop they first appeared on (even to adjacent outcrops only a few metres away; the entire census area was isolated by at least 10 m of sand from adjacent reefs), I am confident that mortality accounted for virtually all of the observed losses of the age-class of juveniles used in the mortality analyses (<34 d since appearance).

The importance of settlement patterns to the population dynamics of the bluehead wrasse depends entirely upon the degree to which juvenile mortality is independent of density. If juvenile mortality were strongly density dependent, the large fluctuations in the supply of recruits over time and space could be sufficiently damped so that the ultimate distribution and abundance of this species would either be uniform or reflect limitations by factors unrelated to settlement. If mortality is proved to be independent of density, then the patterns of settlement observed (both on a temporal and spatial scale) could be expected to persist into the adult population relatively unchanged. Victor (1983*a*) used this reasoning to propose that juvenile mortality rates in bluehead wrasses were not strongly affected by density, since the age structure of the adult population directly reflected the temporal pattern of larval settlement the previous year. Experimental evidence for the density independence of juvenile mortality exists for at least one coral reef fish. Doherty (1983*a*) demonstrated that the removal of resident damselfishes on patch reefs on the Great Barrier Reef did not increase the survival of new juveniles. In addition, experimental increases in juvenile densities on artificial patch reefs did not result in significantly increased rates of mortality (Doherty 1982).

My analysis of natural mortality rates of bluehead wrasse juveniles indicated that there was no significant effect of the number of resident juveniles on the mortality rate of either new recruits or young juveniles. The study included the period with the highest juvenile density recorded in the 4 yr for which I have data on the population size in the study area. Recruitment into the adult population of bluehead wrasses is thus likely to be simply the number of larvae settling minus a standard percentage lost during the juvenile phase. The close correspondence between recruit and adult densities on each of the reefs studied (spatial scale) as well as between the timing of settlement peaks and the subsequent age composition of the adult population on a patch reef (temporal scale; Victor 1983*a*) suggests, furthermore, that density-dependent processes are not significantly affecting adult populations. These findings, taken as a whole, support the hypothesis that the observed distribution and abundance of bluehead wrasses in the San Blas Islands are a direct product of the oceanographic processes that control the temporal and spatial patterns of larval settlement.

Population limitation

Although larval recruitment can be shown to be extremely influential in determining the distribution and abundance of reef fish populations, a caveat is necessary for the term "recruitment-limited." Both the recruitment rate and the actual magnitude of subsequent juvenile mortality determine the ultimate input into the adult population. Which of these two factors is primarily responsible for maintaining a population below its adult carrying capacity is not usually obvious. In the case of an abundant species with high recruit-

ment rates and a high rate of juvenile mortality, it is certainly possible that if there were less or no juvenile mortality, a population that is normally below adult carrying capacity would increase beyond its carrying capacity. It would not be appropriate to label the population below carrying capacity as simply recruitment-limited, for it is the intensity of juvenile mortality that is the main contributor to the reduction of the population of adults below the level at which resource limitation may operate. Nevertheless, the limited supply of recruits also plays some role in depressing the population, since it is only because the recruitment rate is limited that normal juvenile mortality rates keep the adult population below the carrying capacity. An increase in the recruitment rate could make up for the losses to mortality and push the adult population over carrying capacity. Clearly, limitation cannot always be ascribed to a single factor.

A graphic model can demonstrate the relative importance of larval recruitment, juvenile mortality, and adult resource supply to population regulation (Fig. 10). The model describes the controls on the input of individuals to the adult population, concentrating on processes occurring during the early life history. The life of the fish is divided into three phases with two transitions, one from larva to juvenile (=recruitment) and the second from juvenile to adult. Juveniles of many reef fishes, including bluehead wrasses, tend to have distinctly different patterns of both food and habitat utilization from adults (e.g., Sale et al. 1980, Shulman 1985*a*), which justifies treating them as a separate life history phase subject to different limitations. Primary recruitment limitation exists whenever the input of settling larvae is absolutely less than the number of adults the available resources can support (Fig. 10). Juvenile mortality is then only a secondary limiting factor, since all it can do is lower the population even further below its potential carrying capacity. Secondary recruitment limitation exists when the number of larvae settling would be sufficient to reach adult carrying capacity without any juvenile mortality, but juvenile mortality reduces these numbers to below the carrying capacity. In these cases, the input into the adult population is controlled by juvenile mortality, but ultimately limited by the number of settling larvae, since an increase in the number of recruits could compensate for the effect of juvenile mortality. Recruitment limitation ceases to operate when the combined effects of recruitment and juvenile mortality still do not maintain the adult population below its carrying capacity. Any increase in the number of recruits then has no effect on the adult population, which is controlled by other factors, such as the supply of resources.

Primary or secondary recruitment limitation can occur when juvenile mortality rates are density independent (slope of population decay changes in direct proportion to number of recruits, Fig. 10), or even in some cases when juvenile mortality rates are density dependent (slope changes more than changes in number of recruits). However, when density-dependent juvenile mortality rates compensate entirely for increases in recruitment, populations are limited solely by juvenile mortality rates. Although the few studies directly assessing juvenile mortality rates in coral reef fishes have indicated that they are density-independent, there are some indications that density dependent behavioral interactions between some juvenile coral reef fishes could result in density-dependent juvenile mortality (Shulman 1984, 1985*b*). Completely compensatory juvenile mortality has yet to be observed in any coral reef fish population.

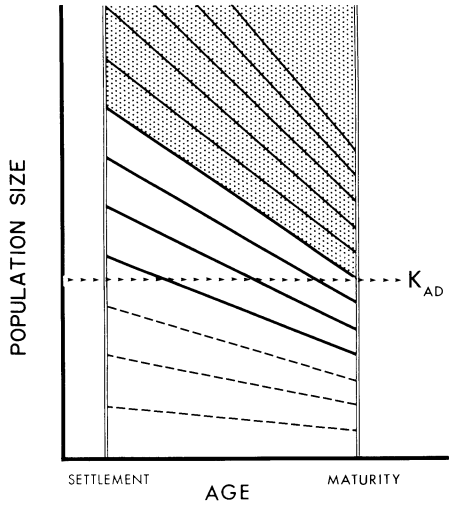

FIG. 10. Graphic model of population limitation of a reef fish. Dashed lines represent population decay in a primary recruitment-limited population; the solid lines in the open area represent population decay in a secondary recruitment-limited population. The population decay lines within the shaded area represent populations that will be limited by processes occurring within the adult stage. The juvenile mortality rate in this example is assumed for clarity to be linear and density independent (50%). K_{AD} = adult carrying capacity.

Without direct information on the carrying capacity of fishes on coral reefs, it is difficult to decide whether cases of recruitment limitation among reef fishes are primary or secondary. The studies that have demonstrated recruitment limitation have involved abundant species with relatively high recruitment rates (Williams 1980, Doherty 1983*a*, Victor 1983*a*, and this study). It is therefore possible that these species may be only secondarily recruitment limited. It is important to note that recruitment limitation has been demonstrated for species which, because of their dependence on the substrate for food, their pronounced territoriality (damselfishes), and their notable abundance (damselfishes and wrasses), would be among the most likely of reef fishes to be limited by resources. Recruitment limitation, especially primary recruitment limitation, is probably most typical of uncommon species with generalized habits. Species with very specialized and ob-

ligate habitat or food requirements may prove to be truly resource limited.

Several invertebrate communities appear to be controlled in large part by recruitment processes (e.g., Sutherland and Karlson 1977, Underwood et al. 1983, Keough 1984*a*). The epifauna on *Pinna* shells in Australia seem not to be limited by resources, predators, or disturbances, and total living cover is consistently <40%. The composition of this assemblage directly reflects the relative rates of recruitment of the members of the assemblage (Keough 1984*a*). The low abundance of epifaunal organisms is attributed to consistently low recruitment of planktonic larvae (Keough 1983, 1984*a*). The same invertebrate assemblage on nearby pier pilings (much larger patches than *Pinna* shells) is characterized by high cover and regulated by competitive interactions, leading Keough (1984*b*) to propose that recruitment-dominated assemblages are characteristic of small and patchy habitats. Coral reef fish assemblages may be recruitment limited for a similar reason (although on a much larger scale). Since coral reefs typically occur as small and relatively isolated patches in a very large tropical ocean, only fishes with planktonic propagules could have initially colonized reefs and subsequently persisted without suffering progressive local extinctions. This dependence on planktonic larvae for reproduction combined with consistently severe and highly variable larval mortality in the plankton could result in chronically recruitment-limited populations.

Regulation of population sizes by recruitment rates rather than by resource supplies should not be misconstrued to mean that competition does not occur among coral reef fishes and that coral reef fish species are therefore generalists and perhaps even ecologically equivalent. The lottery hypothesis, as originally formulated (Sale 1978), was often interpreted to imply these things, and prompted a number of dissenting papers documenting coral reef fish species that do have particular habitat preferences (Robertson and Lassig 1980, Waldner and Robertson 1980, Anderson et al. 1981). Recruitment limitation hypotheses are, however, profoundly different from the lottery hypothesis which assumes space limitation of populations (Doherty 1983*a*; Thresher 1983 confuses the two hypotheses). All recruitment limitation does mean is that the absolute size of fish populations is determined by settlement rates and is not a product of competitive interactions on the reef. Competitive interactions that do not directly reduce population sizes could still affect individual fitnesses within recruitment-limited populations, as long as some individuals in the population predictably obtain different amounts of resources as a result of these interactions. This process could lead to habitat specializations within a species and habitat partitioning between species. However, if the outcomes of interactions are not predictable, the effects, even if major, would not affect the evolution of organisms ("epiphenomena," sensu Underwood et al. 1983). Whether competitive interactions have molded the characteristics of reef fishes is a controversial subject (Sale 1980, Gladfelter and Johnson 1983, Warner 1984).

Recruitment limitation has important implications for the coexistence of potentially competing species. If the ultimate source of larval mortality in the plankton proves to be interspecific competition for some limited planktonic resource (at present unknown), then the mechanisms allowing for coexistence must occur within the larval stage. If, however, larval competition is not the ultimate arbitrator of survival in the plankton, then it can be assumed that when populations are limited by recruitment, resources are not in short supply and competitive interactions can, at most, only affect individual fitnesses and not population numbers. Superior competitors then cannot translate their success into reduced numbers of their competitors and competitive exclusion (the extinction of inferior competitor species) does not take place. The immense diversity of fishes on Indo-Pacific coral reefs (>2000 species are known to coexist on reefs in the Philippines [Sale 1980]) could therefore be perhaps the most eloquent evidence for the prevalence of recruitment limitation among coral reef fish populations.

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