

LARVAL SETTLEMENT AND JUVENILE MORTALITY IN A RECRUITMENT-LIMITED CORAL REEF FISH POPULATION¹

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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 km², 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 km², 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 1984a). 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, 1983a for damselfishes and Victor 1983a 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, 1983b, 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 1983a), 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, $\approx 12 \times 8$ 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 km² 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-m² 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 km²) 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 m² (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 1983b). This period of hiding results in the

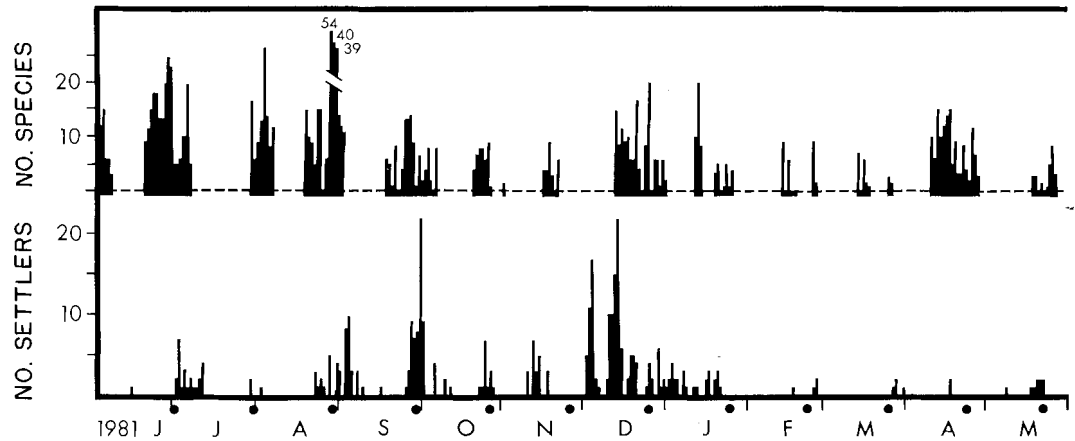


FIG. 1. The daily pattern of planktonic larval diversity (upper) as measured by the number of species of reef fish larvae captured at a night-light, compared with the daily pattern of bluehead wrasse recruitment onto a number of isolated coral outcrops (lower) over a period of 18 mo in the San Blas Islands. 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 as 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

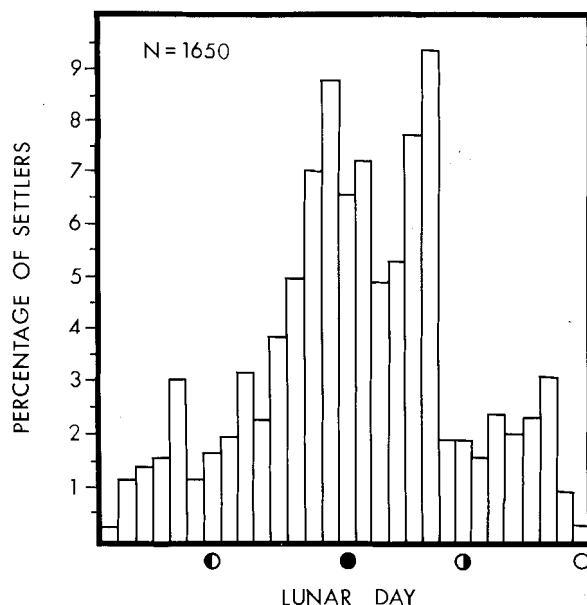


FIG. 2. Frequency distribution of larval settlement by lunar day. ● = new moon, ○ = full moon.

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 1983a).

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.

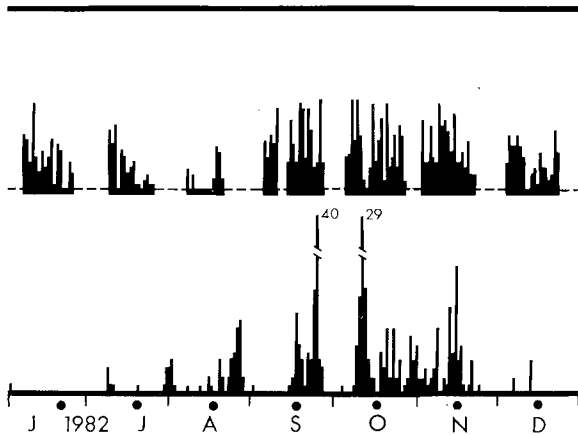


FIG. 1. Continued.

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/m² 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-

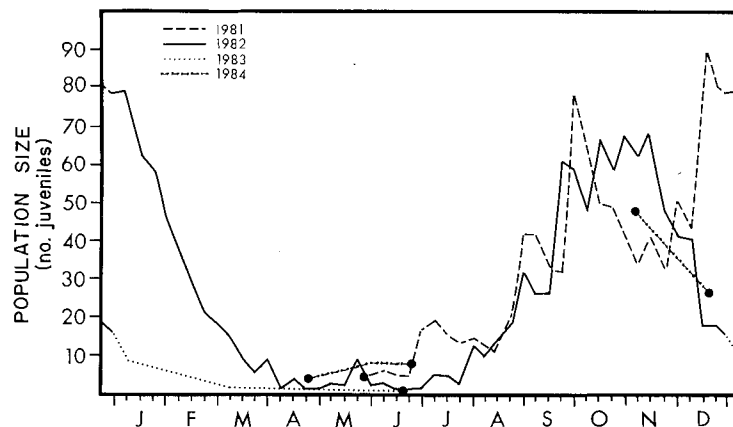


FIG. 3. The annual cycle in the total size of the juvenile population within the daily census area on Ukubtupo Reef.

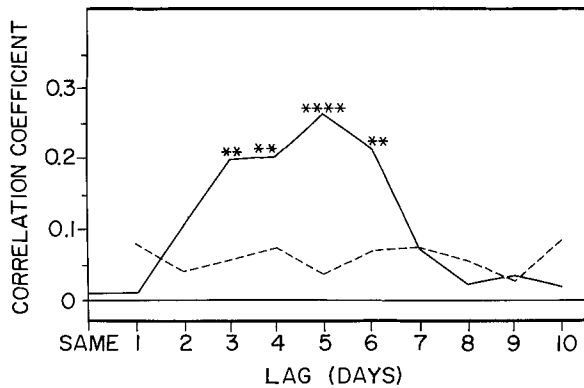


FIG. 4. Correlates of the number of bluehead wrasse recruits appearing per day. -- the correlation coefficients between the number of bluehead wrasse appearing on the reef and the number of resident juveniles disappearing on the same day and on each day up to 10 d before the day of the appearances. — 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 km², 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-

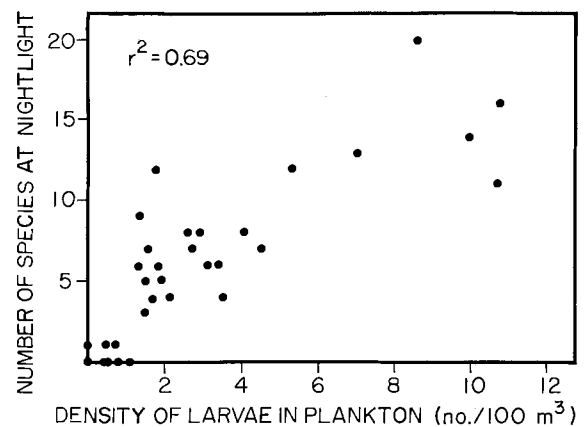


FIG. 5. Relationship between the number of reef fish larval species captured at a night-light and the density of reef fish larvae in the plankton (measured with plankton tows) on the same night.

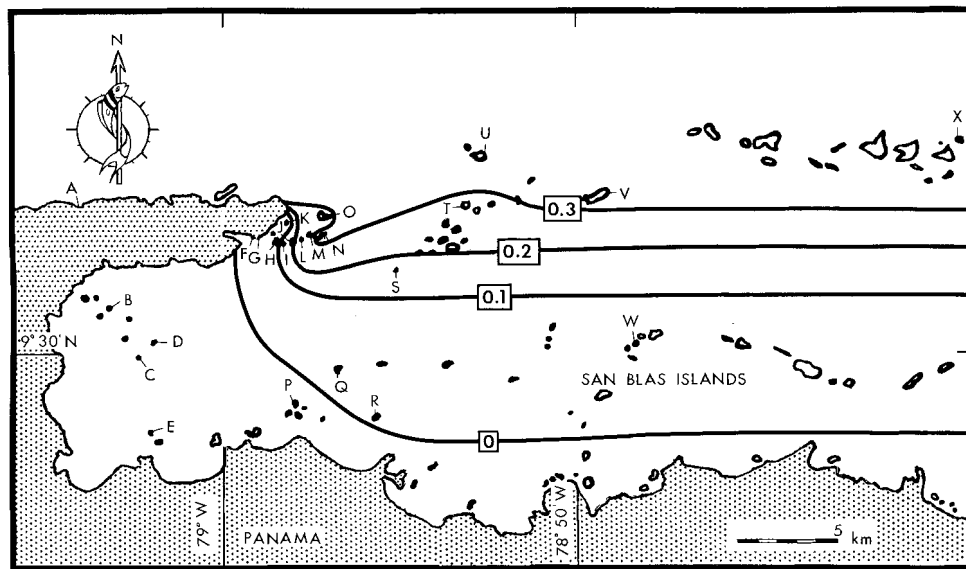


FIG. 6. Map of the San Blas Islands of Panama showing isopleths of juvenile densities (number per square metre) recorded in January 1983. The prevailing current recorded over several years at a reef near site L was from 1° west of due north. A: Puerto Geladi, B: Mandinga, C: Bajo Tridente, D: Mandinga, 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 $\approx 3\%/d$ on day 4 and then showed a gradual downward trend. After 3 wk, mortality had fallen to $\sim 1\%/d$, 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.

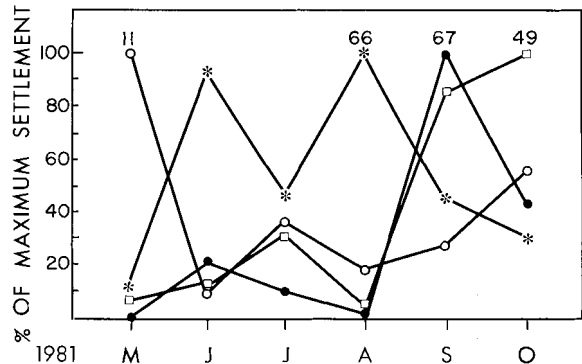


FIG. 7. Variability in settlement among four sites within 1 km² over 6 mo. □ Ukubtupo, ○ Vieja reef, ● Aguadargana, • Snapper reef. The numbers at each maximum represent the number of recruits on the maximum settlement month for each site.

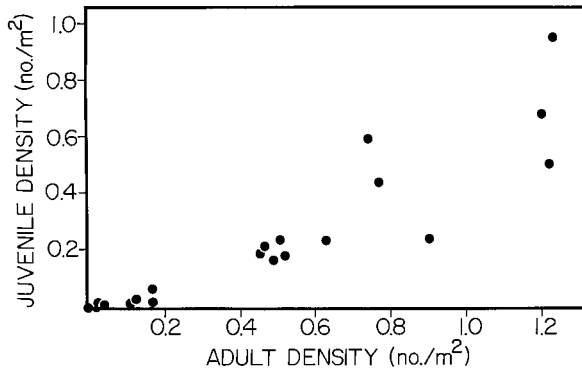


FIG. 8. Relationship between adult bluehead wrasse density and juvenile density recorded in January 1983 on 24 reefs in the San Blas Islands of Panama. Four reefs are represented at the origin.

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 \approx 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 equilibrium 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			
	<i>n</i>	Mean SL (mm)	Mean age (d)	<i>n</i>	Mean SL (mm)	Mean age (d)	<i>n</i>	Mean SL (mm)	Mean age (d)	<i>n</i>	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
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).

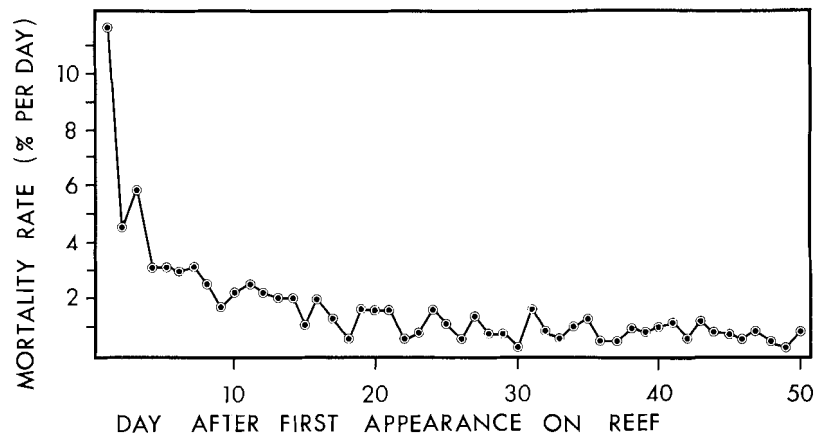


FIG. 9. Daily mortality rates of juvenile bluehead wrasses within the daily census area on Ukubtupo Reef. Mortality rate is defined as the percent of a settling cohort disappearing each day.

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 1983b). In subtropical areas where the relationship between spawning and settlement seasons is strong (Doherty 1983b) 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 1983a), 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 because of turbulence, as suggested by Doherty (1983b). 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		Chi-square
	Ex-pected	Ob-served	
Sand	21	0	61****
Sponge	11	1	
Colonial anemone	14	0	
Dead coral	112	155	
Live coral	57	59	
Dead <i>Millepora</i> spp.	30	8	46****
Dead <i>Acropora palmata</i>	95	95	
Dead <i>Montipora</i> spp.	10	27	
Dead <i>Agaricia</i> spp.	20	25	
Live <i>Millepora</i> spp.	30	44	17****
Live <i>Acropora palmata</i>	7	0	
Live <i>Montipora</i> spp.	4	1	
Live <i>Agaricia</i> spp.	18	14	
0-2 m	85	185	209****
2-4 m	21	20	
>4 m	110	10	

**** $P < .0001$.

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, 1983a, 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, 1983a, Victor 1983a, 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 1983a). 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 (1983a) 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, 1983a, Victor 1983a). However, observed settlement rates could also be a product of predator densities (Shulman et al. 1983, Shulman 1985a), physical disturbances, or competition between taxa (Shulman et al. 1983, Shulman 1985b). 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

