

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

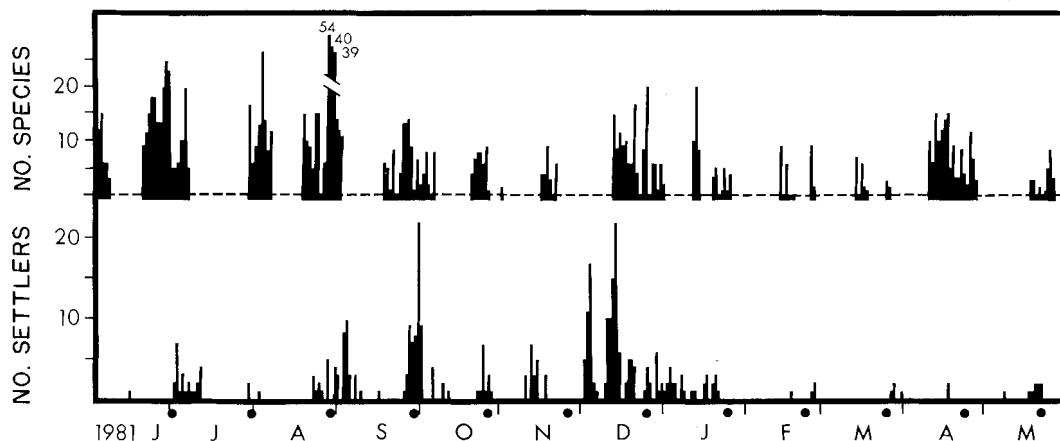


FIG. 1. The daily pattern of planktonic larval diversity (upper) as measured by the number of species of reef fish larvae captured at a night-light, compared with the daily pattern of bluehead wrasse recruitment onto a number of isolated coral outcrops (lower) over a period of 18 mo in the San Blas Islands.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

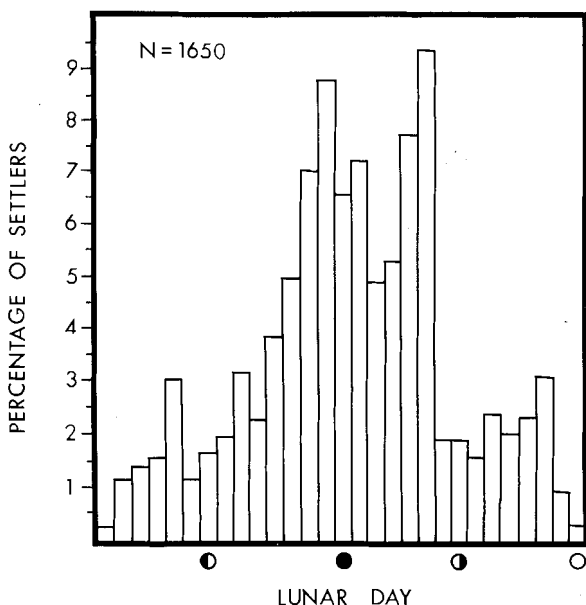


FIG. 2. Frequency distribution of larval settlement by lunar day. ● = new moon, ○ = full moon.

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.

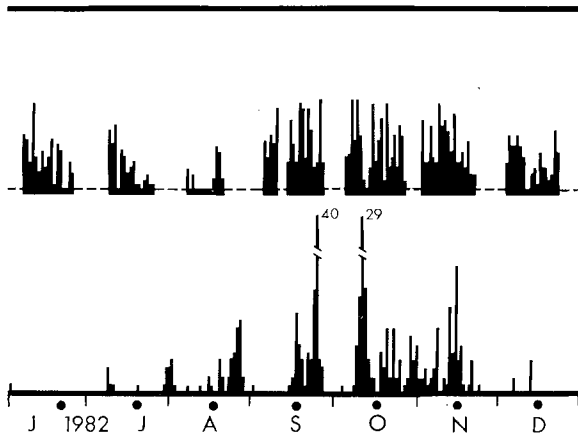


FIG. 1. Continued.

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-

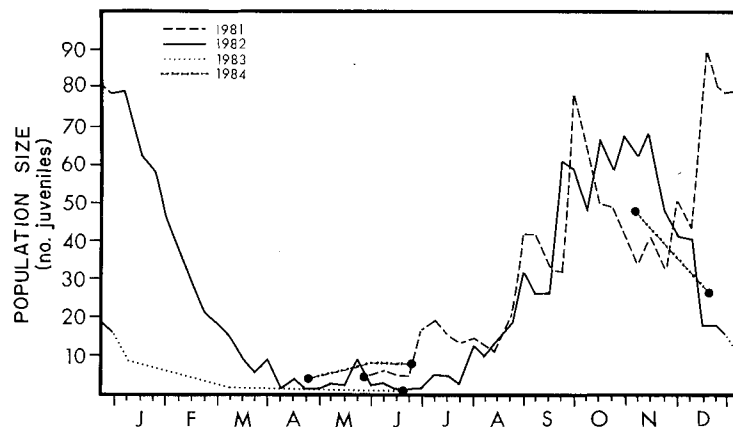


FIG. 3. The annual cycle in the total size of the juvenile population within the daily census area on Ukubtupo Reef.

