Recruitment and Population Dynamics of a Coral Reef Fish

Abstract. *Daily otolith increments were used to determine the daily pattern of settlement of the bluehead wrasse (*Thalassoma bifasciatum*), a Caribbean coral reef fish. Recruitment occurs in brief and sporadic episodes even though bluehead wrasses spawn every day. Patterns of recruitment do not correspond to patterns of mortality on the reef. The composition of the adult population directly reflects the relative rates of recruitment of juveniles the year before. The population dynamics of this species may therefore be determined by the supply of recruits and not by the supply of space or some other resource on the reef.*

Virtually all coral reef fishes settle onto the reef after spending some time as planktonic larvae (*1*). This process of recruitment is one of the most important and yet least studied aspects of reef fish ecology. Recently, some descriptions of settlement patterns have been reported (*2*). However, many questions are unanswered, such as what determines patterns of recruitment and what impact these patterns have on adult populations. I report that recruitment in the bluehead wrasse, *Thalassoma bifasciatum*, occurs in brief and sporadic episodes that are not related either to patterns of reproduction or to mortality on the reef. Furthermore, I show that these brief episodes of recruitment can have a profound impact on adult populations in the future. These findings are incompatible with the view that reef fish communities are stable and primarily limited by resources (*3*).

It has been suggested that recruitment patterns of coral reef fishes closely parallel spawning patterns and are thus predictable (*4*). This may be true for species with infrequent and sharply defined spawning bouts, because outside of spawning periods, eggs are not being produced and larvae are not available for settlement. However, how much of the variability in recruitment is due to reproductive patterns and how much to other processes can be elucidated by examining a species that spawns every day. Daily spawning is a common phenomenon among coral reef fishes, particularly in the wrasses (Labridae), parrotfishes (Scaridae), and the basses (Serranidae) (*5*). I examined recruitment of the bluehead wrasse on coral reefs in the San Blas Archipelago, on the Caribbean coast of Panama, where the daily spawning behavior of the species has been monitored for many years.

I used the daily otolith increment technique (*6*) to calculate the pattern of settlement. Since there are daily lines and a prominent transition mark corresponding to settlement on the otoliths of the bluehead wrasse (*7*), the settlement pattern of populations of fish, including adults, can be easily reconstructed. The date of settlement of each individual is obtained by subtracting the number of lines after the settlement mark from the date of capture. For this study I collected 103 juveniles from a large patch reef near the island of Porvenir in late 1980.

Recruitment of bluehead wrasses occurred in brief and sporadic episodes (Fig. 1) (*8*) and did not reflect the daily spawning pattern of this species. It has been reported that reef fishes are limited by the availability of resources such as space and that recruits settle from a pool of superabundant larvae into spaces made available by the death of residents (*3*, *9*). According to these views, the brief episodes of settlement of bluehead wrasses would be in response to sudden die-offs among the reef population. Mortality rates of bluehead wrasses on patch reefs around the study area were monitored (*10*). To prevent recruitment, newly settled fish were continuously removed; at the same time changes in the adult population were monitored by monthly censuses. Populations declined somewhat steadily (86.5 percent survival per month; standard deviation, 6.7 percent; $N = 8$ censuses). During the monitoring period occasional large peaks of settlement occurred on these and surrounding reefs without corresponding changes in the mortality rate. It is likely that some process occurring in the plank-

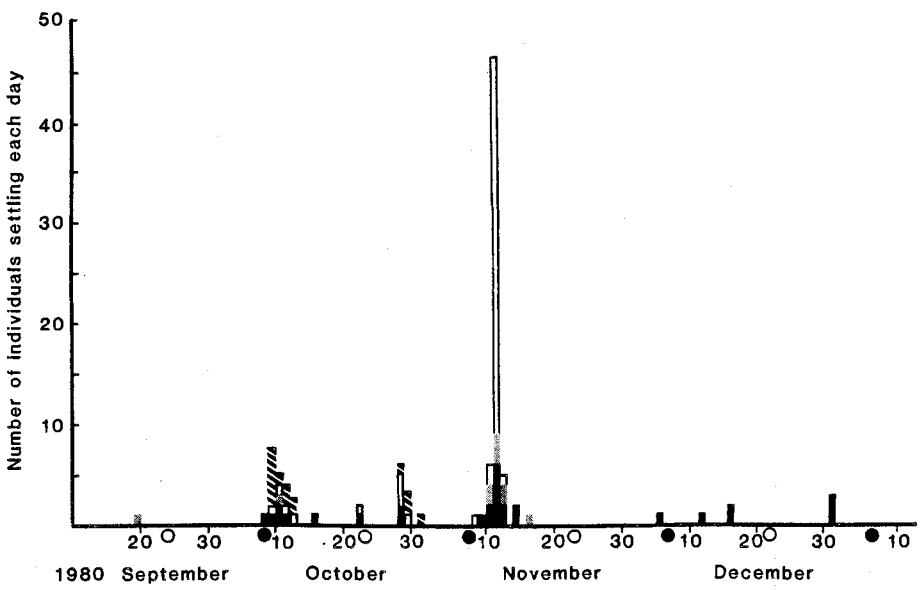

Fig. 1. The recruitment of juvenile *Thalassoma bifasciatum* onto a single patch reef in the San Blas Islands, Panama. Bars represent the number of individuals that settled each day, calculated by subtracting the age since settlement from the date of capture for each individual. Hatched bars represent fish caught in early November 1980, open bars those caught the third week of November, shaded bars those caught in late December, and solid bars those caught in early January. Solid circles denote new moon and open circles, full moon.

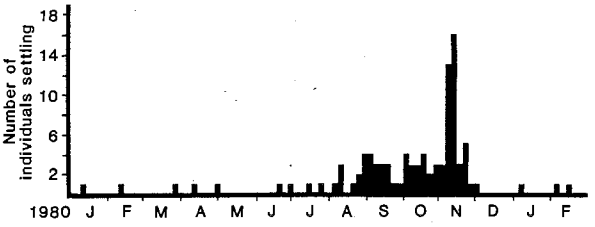

Fig. 2. The pattern of recruitment for 98 adult *Thalassoma bifasciatum* from a single patch reef in the San Blas Islands, Panama. Bars represent the number of individuals that settled in each 5-day period throughout 1980. Collections were made in July 1981. The date of settlement for each individual was calculated as described in the legend to Fig. 1.

ton is responsible for the pattern of settlement of the bluehead wrasse.

The importance of recruitment patterns depends on their impact on populations in the future. If the recruitment pattern calculated from the adult population does not exhibit the same characteristics as were shown by collections of juveniles the previous year (*11*), it could be presumed that the dynamics of the population as a whole are being determined by factors independent of recruitment. If, however, the recruitment pattern calculated from adults matches closely the recruitment pattern calculated from juveniles, it would indicate that the dynamics of the population may be determined at the settlement stage (*12*). In order to resolve this question I collected 98 adult bluehead wrasses in August 1981, from a reef adjacent to the one from which I had collected the juveniles the year before.

The pattern of settlement calculated from the adults strongly paralleled the pattern obtained from juveniles the previous year (Fig. 2). Over one-third of the entire adult population settled during the mid-November peak of settlement, and an additional 25 percent settled during October. The composition of the adult population appeared to result from the pattern of settlement of larvae the year before.

The pattern of recruitment can affect the size of future populations. If the composition of the adult population reflects the rates of recruitment, and if mortality is steady and recruitment is erratic (the number of bluehead wrasses recorded to be settling in a single week ranged from 0 to as high as 54 percent of the entire reef population), then variability in recruitment is responsible for fluctuations in the size of the population. The absolute size of the population is determined both by recruitment rates and by the actual rate of subsequent mortality (*12*). If recruitment rates are not sufficient to enable the population to reach the carrying capacity of the habitat, then the population is limited by recruitment (*13*).

Populations of bluehead wrasse are subject to dramatic fluctuations in size. Censuses of patch reef populations in Panama taken yearly during the past 6 years show that population sizes often vary in magnitude from three- to fivefold from year to year. Densities on one reef changed 706 percent between 1976 and 1980 (*14*).

In summary my findings show that bluehead wrasse larvae settle onto coral reefs in brief and sporadic episodes even though this species spawned every day. This indicates that the pelagic environment had a severe and unpredictable effect on the relationship between reproduction and recruitment. Because recruitment did not reflect patterns of mortality on the reef, the findings do not support the view that reef fish populations are resource-limited. Rates of recruitment apparently determine a large part of the population dynamics of the bluehead wrasse and thus may be the ultimate determinant of the effects of competition and predation on the community structure of coral reefs.

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References and Notes

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6. Otoliths, which are stone-like calcium carbonate accretions in the semicircular canals of bony fishes, function as aids in balance and sound perception. The relatively new technique of aging by daily otolith increments is not widely used but is valuable for recruitment studies [E. B. Brothers and W. N. McFarland, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **178**, 369 (1980)].
7. B. C. Victor, *Mar. Biol.*, in press.
8. In time mortality can result in an increasing underestimation of the magnitude of recruitment peaks the further back one extrapolates from the collection date. This distortion was not strong enough to affect the pattern of settlement since the last collection exhibited the same pattern as those made earlier. More than half the juveniles captured in January had settled during the early November peak.
9. D. R. Robertson, S. G. Hoffman, and J. Sheldon [*Ecology* **62**, 1162 (1981)] draw a different conclusion than other investigators (*3*).
10. B. Victor and R. R. Warner, unpublished data.
11. Bluehead wrasses are short-lived: maximum longevity is 3 years and the average age of adults is about 1 year (B. C. Victor, unpublished data).
12. In addition to settlement factors, mortality after settlement affects population sizes. Because the composition of the adult population in this study directly reflected the rate of recruitment, mortality was constant and independent of density.
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14. R. R. Warner and S. G. Hoffman, unpublished data.
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