PRIORITY EFFECTS IN JUVENILE CORAL REEF FISH RECRUITMENT

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Abstract

Two kinds of priority effects are reported for coral reef fish on experimental reefs: 1) A significant decrease in recruitment of two species of settling juveniles occurs in the presence of a resident territorial damselfish. 2) Prior settlement of a juvenile predator lowers successful recruitment of two juvenile prey species. The first effect increases determinism in the structure of coral reef fish assemblages while the second increases their unpredictability.

Priority effects, in which the presence of one species in a habitat decreases the probability of invasion by another, have been hypothesized to be of importance in maintaining high regional species diversity and determining local species distributions (1,2). One species can lower the juvenile recruitment of another in several possible ways. A) Competition: Adult residents or settling juveniles can actively interfere with juvenile settlement through aggression (interference competition) or passively influence settlement by altering or co-opti resources (exploitative competition). B) Predation: Predatory residents can decrease recruitment by preying on juveniles, or, evolutionarily, selecting for settlement in areas not occupied by predators. Predatory juveniles settling first can similarly prevent subsequent successful recruitment by prey species. These mechanisms are not mutually exclusive and there are examples of at least two of them operating together (3).

The existence of priority effects among coral reef fish would have significant implications for our understanding of the processes controlling these assemblages, a subject of much current controversy. The controversy centers on whether fish assemblages are structured by deterministic competitive and predatory interactions or by stochastic recruitment of juveniles into unpredictabl available space (4). Priority effects between residents and juveniles, in which residents control the species identity of juveniles recruiting into the local habitat, suggest that assemblage composition is more deterministic. Juvenile-juvenile priority effects, in which order of settlement determines local species composition, suggest an unpredictable assemblage structure, strongly controlled by the vagaries of settlement of juveniles from planktonic larvae. The importance of order of settlement in determining community structure has been shown for sessile organisms in experimental space-limited systems (2), but has not yet been documented for mobile species. In this study, we report the existence of two kinds of priority effects among coral reef fish assemblages, a system involving mobile species with strong behavioral interactions.

The present study was conducted utilizing the facilities of the NULS-1 Hydrolab operated by NOAA on St. Croix, U. S. Virgin Islands. The underwater habitat ~~Hydrolab~~ is located in Salt River Canyon, a 70-100 m wide submarine canyon flanked by two coral reef walls. Thirty artificial reefs, each consisting of eleven construction blocks placed in a pyramid two blocks wide and three blocks high, were built on the sand/seagrass (*Halophila decipiens*) floor of the canyon at a depth of 16 to 20 m. Ten replicate reefs were constructed at each of three different times: four weeks ("old" reefs), two weeks ("intermediate" reefs) and one-half day ("young" reefs) prior to the start of the July 7 - July 13, 1979 Hydrolab mission. The reefs were placed in a grid pattern with a minimum distance of 5 m between them (5). All the fishes on the artificial reefs were visually censused by two observers approximately twice weekly before the mission and several times daily during the mission (6). Weekly censuses continued following the mission until the artificial reefs were destroyed by Hurricanes David and Frederic in late August and early September, 1979. Due to the abrupt, early termination of this study, the results reported here were observed over only a short period of time.

A total of 44 species colonized the artificial reefs; 24 of these were found on at least five reefs (7). The colonization curves (Fig. 1) show that numbers of individuals and species increase monotonically to an asymptote on young and intermediate reefs but overshoot their asymptotic values on the old reefs. The three sets of reefs differ significantly in both numbers of species and numbers of individuals (excluding grunts, Haemulidae (9)) recruited in the first twelve days after each set was built (ANOVA; $p < .001$). Young reefs recruited the fewest individuals and species and old reefs the most. This may represent a seasonal decrease in number of juvenile fish settling from the plankton (9), or be due to a dilution effect, there being only ten reefs present to which fish could recruit during the twelve days following construction of the old reefs but twenty for the intermediate reefs and thirty for the young reefs.

At any given time, reefs that had been in the water longer had higher resident fish populations. During the period of intensive censusing, from 7/8 to 7/19, net recruitment (10) to the three different aged sets of reefs was compared. The youngest reefs, with the lowest resident populations, showed the highest rate of net recruitment of individuals and species with intermediate and old reefs having significantly lower net recruitment rates (ANOVA; $p<.05$) (11). This difference is reflected in the colonization curves for both individuals and species which appear to reach an asymptote after approximately one month (Fig. 1)

There also exist species differences in net recruitment to different aged reefs; grunts (Haemulidae), tobaccofish (*Serranus tabacarius*), cardinalfish (Apogonidae), and sharpnose puffers (*Canthigaster rostrata*) showed significantly higher net recruitment to young, relatively unoccupied reefs while no such significant difference was found for mahogany snappers (*Lutjanus mahogoni*), yellow-tail snappers (*Ocyurus chrysurus*), black-fin snappers (*Lutjanus buccanella*), high-hats (*Equetus acuminatus*) and surgeonfish (*Acanthurus bahianus* and *A. chirurgus*) These may reflect differences between species in ability to settle and survive on occupied reefs or major, and important, differences in recruitment strategies.

To determine the effect of a resident on recruitment, one adult beaugregory (*Eupomacentrus leucostictus*), a territorial damselfish, was transplanted onto each of five of the ten replicates for the three sets of reefs on July 7, 1979 (12). Successful recruitment of surgeonfishes (*Acanthurus bahianus* and *A. chirurgus*) and reef butterflyfishes (*Chaetodon sedentarius*) to reefs with beaugregories present was significantly lower relative to reefs which lacked beaugregories (X^2 test; $p<.05$ for surgeonfish, $p<.025$ for reef butterflyfish).

The most common group of piscivorous fish recruiting to the reefs were snappers of the genus *Lutjanus*. The juveniles of two species were represented (mahogany, *L. mahogoni*; black-fin, *L. buccanella*), the mahogany snapper being more abundant. These snappers were observed to prey on grunts and presumably attacked other small juvenile fishes. Grunts showed a non-random recruitment pattern relative to the presençe or absence of *Lutjanus* snappers during the first twelve days after the reefs were built. The presence of snappers on a reef significantly decreased the numbers of grunts subsequently recruited while reefs which lacked snappers recruited grunts in numbers slightly greater than expected (X^2 test; $p<.001$).

A similar result was obtained for the relationship between snappers and high-hats. High-hats only settled on "full moon reefs" (see below); of these twenty reefs, nine recruited high-hats in the twelve days following construction. No juvenile snappers were present on those reefs before or during the settlement of high-hats, demonstrating a statistically significant negative effect of snapper presence on high-hat recruitment (binomial test; $p<.05$).

The timing of recruitment of planktonic larvae is important if order of settlement affects species coexistence. Old reefs and young reefs were built within three days of full moons and intermediate reefs within three days of a new moon, thus allowing partial examination of lunar periodicity in settlement of juveniles from planktonic larvae (13). Mahogany snappers and *Diplectrum* sp. showed significantly higher recruitment to new moon reefs in the first seven days as compared to full moon reefs ($p<.05$). The data are also suggestive for greater settlement on new moon reefs by black-fin snappers, doctorfish and sharpnose puffers ($p<.10$) (14). Only one species, the high-hat, showed significantly higher recruitment to full moon reefs ($p<.05$), settling only on those reefs. There is also very strong evidence from McFarland, et al. (15) that French grunts (*Haemulon flavolineatum*) have semi-monthly peaks in recruitment.

This study has shown that at least two kinds of priority effects exist in juvenile coral reef fish recruitment. The underlying mechanisms producing these two effects are very different, as are their implications for community structure.

The presence of an adult resident (beaugregory) decreases the settlement of juveniles of two other species. This territorial damselfish has been shown to be extremely aggressive, particularly towards trophic competitors and egg predators (demersal eggs are laid in territories of male beaugregories) (15). On our artificial reefs, the herbivorous beaugregories significantly decreased successful recruitment of surgeonfishes - a family of schooling herbivores. The beaugregories also lowered recruitment of reef butterflyfish - a member of a family known to include fish eggs in its diet (16).

The second kind of priority effect occurs between juvenile piscivores and their prey. The order of settlement is critical; if snappers settle on a reef first, the numbers of successfully settling grunts and high-hats are reduced. The reverse, however, is not true; snappers do settle on reefs already occupied by their prey. It is likely that the prey quickly outgrow the size range in which they are susceptible to predation by newly settling snappers, thus allowing coexistence of these species. This situation is analogous in mechanism and effect to size-limited predation found in temperate intertidal and freshwater communities (17).

The ecological implication of these two kinds of priority effects are diametrically opposed. If residents can successfully exclude certain species from a habitat while allowing the recruitment of others, fish assemblages become more deterministic. The composition of these assemblages can be stable if residents allow their own species to settle while excluding others, "successional" if residents replace each other in a transitive order, and cyclical if multispecies priority effects are non-transitive. In contrast, the existence of predator-prey priority effects, in which order of settlement of juveniles alone determines community composition, introduces a stochastic element into the structure of fish assemblages.

The present controvery about the structure of reef fish assemblages centers on the degree of determinism and stochasticity inherent in the processes that govern this system (4). The data presented here are critical to this issue and suggest the following conclusion: in unoccupied habitat (created by storms, mortality, changes in reef structure), the order of settlement, particularly of predators and prey, will partially determine composition of the initial assemblage; in occupied areas, residents are likely to determine which species can possibly invade, but within this group of "permissible" invaders, order of settlement may determine which will successfully recruit into the habitat.

The order of settlement of juveniles will be influenced by the lunar and seasonal periodicities in settlement patterns. Lunar cycles of settlement are reported here and elsewhere; many studies have also shown seasonality of spawning and settlement of reef fish (18). The timing of settlement of potential prey species relative to their predators can be a crucial factor in successful recruitment into a habitat. The existence of priority effects may have evolutionary significance by producing selection on potential prey for settlement before potential predators.

It is probable that there exist other priority effects, of varying degrees of subtlety, among juvenile coral reef fish. Indeed, our results show that the denser the resident population, the lower the net recruitment to a reef. It is likely that a large number of intra- and interspecific interactions, of which the ones elucidated in this study are examples, combine to produce this result.

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5. Old reefs were built on 6/7/79, intermediate reefs on 6/21/79, and young reefs on 7/7/79. The position of reefs in the grid were determined using rotating block design in the east-west direction and random design in the canyon axis (north-south) direction.

6. Because of the small size and regular structure of these reefs, all fish could be observed with relative ease. Reef fish in general seen unaffected by the presence of an observer after a several minute period of acclimation.

7. Species list and recruitment rates in M. J. Shulman, et al., in prep.

8. Grunts are excluded from this analysis because they far outnumber the total of other species. Analyses which include grunts only reflect the trends in that spe

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10. Net recruitment = change in number of individuals or species from one census to the next.

11. Net recruitment from 7/8 to 7/19: Old reefs - 4.4 ind., 1.2 spp.; Intermediate reefs - 4.4 ind., 1.0 spp.; Young reefs - 9.4 ind., 3.6 spp.

12. An earlier, unsuccessful attempt was made to transplant Eupomacentrus variabilis onto one-half of the reefs; all had disappeared by 7/7/79.

13. Full moons on 6/10/79 and 7/9/79. New moon on 6/24/79.

14. Lunar periodicity of settlement was determined by comparing old plus young reefs with intermediate reefs using the median test analyzed with Fisher's exact probability test.

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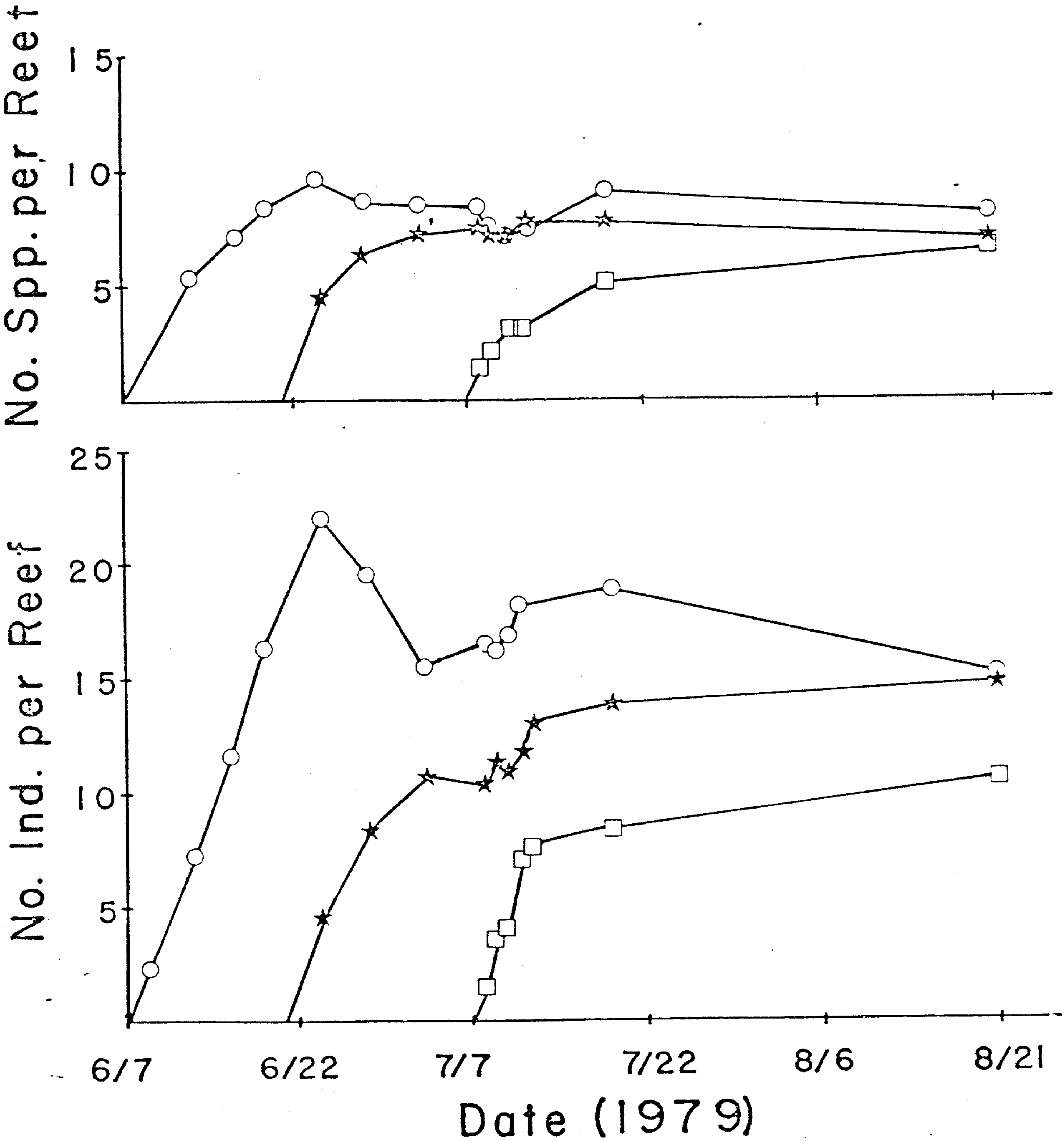
Figure Legends

Cover Photo: Underwater habitat "Hydrolab" located on St. Croix, U. S. Virgin Islands. Hydrolab is funded by the Manned Undersea Science and Technology Office of NOAA and is currently operated by the West Indies Laboratory, Fairleigh Dickinson University. The Hydrolab was used for a study on recruitment in juvenile coral reef fishes. See page __. (Dennis Hubbard, West Indies Laboratory, St. Croix)

Figure 1: Colonization curves of species and individuals on the artificial reefs. Circles represent old reefs, stars intermediate reefs and squares young reefs.



No. Spp. per Reef
15
10
5
No. Ind. per Reef
25
20
15
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5
6/7
6/22
7/7
7/22
8/6
8/21
Date (1979)