DIEL MIGRATION AND DEPTH ZONATION IN A CARIBBEAN CORAL REEF FISH COMMUNITY

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Abstract. The structure of reef fish communities varies with depth and time of day. Along the slope of the reef, habitat "zones" occur with respective changes in surge, ultraviolet light, structure complexity, algal cover, predator and prey abundances, and damselfish territoriality; many of these factors also change with the time of day. Many species and guilds of fish exhibited clear zonation with depth. This may be related to differences in available resources. One reason that some species of herbivorous fish exhibit diel movement across these depth zones may be to take advantage of these different resources available at different times of the day. Depth zonation and vertical migration represent different strategies for partitioning resources spatially and may contribute to the coexistence of species and the maintenance of diversity in coral reefs.

Key Words: Acanthuridae, Scaridae, Pomacentridae, algivores, herbivores, planktivores, piscivores, depth zonation, diel movement, reef fish, vertical migration.

INTRODUCTION

Coral reefs exhibit varying zonation, ranging from the breaker zone to below the mixed reef zone. In shallow depths, near the reef crest, wave surge and light intensity are high. At greater depths, the reef faces less surge and lower light intensity. These intensities also change throughout the daylight hours, with the least intensity occurring at dawn and dusk, and peaking in intensity mid-day. In addition, the structural composition of coral changes from greater complexity at shallower depths, to less complexity at greater depths.

Coral reef fish communities contain numerous coexisting species on the reef slope. Many of these species belong to the same feeding guild and need similar refuge spaces. If fish abundance is high enough to make these resources limiting, these refuges and feeding grounds may be obtained through inter- or intraspecific competition. Territorial damselfish constitute one example of shallow-water competition for resources as damselfish aggressively defend territories both inter- and intraspecifically.

Alternatively, spatial and temporal partitioning of resources may provide the mechanism allowing for species coexistence on coral reefs. The combination of patchily distributed resources and predictable diel variation in abiotic and biotic factors such as UV light and surge throughout the reef may provide an environment in which diel migrations optimize a species' fitness by allowing access to a greater variety of resources than if it were to remain in one area. The striped parrotfish provides an example of a diel vertical migrator on the reef surface (Ogden and Bucknan, 1973).

We hypothesize that coexistence of the diverse fish assemblage on Discovery Bay's coral reef results from partitioning of resources on a spatial and temporal scale. If reef fish do partition food resources, we expect fish of the same feeding guilds to exhibit varying diel migratory patterns.

METHODS

Fish abundances were recorded between 1 - 8 March 1996 on the west fore reef near dive site M1, Discovery Bay, Jamaica. Four transects were haphazardly established: one each at 1.5 m, 4.6 m, 9.2 m, and 13.8 m. Fish censuses were performed using a timed strip transect technique (Sanderson et al 1986): two snorkellers (1.5 m and 4.6 m depths) and two scuba divers (9.2 m and 13.8 m) swam parallel to the reef crest at a uniform and standardized swimming speed for ten minutes. One observer per transect recorded all parrotfish and wrasse present in a 5 m wide swath, while the other observer recorded all other species of fish in the same 5 m swath. Fish censuses at all four depths were repeated for each of three time periods: morning (0815 - 0845), midday (1330 - 1415), and evening (1715 - 1800).

The abundances of each species were recorded. In addition, juveniles, adults, and supermales were

recorded separately for those species in which size and coloration distinguished between the age classes (Table 1). Threespot damselfish, dusky damselfish, cocoa damselfish and Beaugregorys were grouped because they could not be distinguished from one another. Striped and princess parrotfish could not be distinguished in the juvenile and adult stages and hence were group as one species. Those less than 10 cm were recorded as juveniles and those greater than 10 cm as adults. For all species, adults and supermales were combined for analysis. Supermale abundance data from 9.2 m and 13.8 m were accidentally lost after being combined with midphase adults; however, striped and redband supermale parrotfish at 1.5 m and 4.6 m transects were analyzed to determine shallow water diurnal abundance patterns for this age class. Species were also assigned to feeding guilds (based on Randall 1967): herbivores (including algivores), piscivores, crustacivores, invertivores, planktivores, and coralivores. Effects of depth and time on abundance of individual species and guilds were analyzed with two-way ANOVAs.

Reef structure and substrate cover were quantified at each depth. Complexity and cover were assessed at the start of the transect and at locations reached at 3, 6, and 10 min along each transect. Complexity was calculated as $(1 - d / l)$ where d = the straight-line distance between the ends of a chain draped over the reef contours and l = the length of chain (5 m). We estimated th percent cover of live coral, hard substrate, sand, macroalgae (that appearing 3-dimensional), and microalgae (that lying flat on substrate, thin) under each 1 m segment of chain for the length of the chain. Complexity and reef cover type were averaged for each depth. Complexity and reef cover types were then compared at various depths using a one-way ANOVA or Kruskal - Wallis ANOVA for ranks.

RESULTS

The abundances of 22 of 31 groups of fish varied significantly with depth (Table 1). Piscivores were significantly more abundant at 13.8 m throughout the day, although there was a marked decrease in total piscivore abundance at mid-day ($F = 8.60$, $df = 1$, $p = 0.007$; Figures 1c and 3). Herbivores and algivores were significantly more abundant in shallow water (1.5 m and 4.6 m) than deep (9.2 m and 13.8 m) ($F = 41.2$, $df = 1$, $p < 0.001$ and 95.5, $df = 1$, $p < 0.001$ respectively; Figures 1a and 1b respectively). Planktivores were significantly more abundant at 13.8 m, and abundance increased throughout the day ($F = 15.8$, $df = 1$, $p < 0.001$, Fig. 2). Invertivores were significantly more abundant in shallow water than at depth. ($F = 32.6$, $df = 1$, $p < 0.001$; Figure 1d).

Members of the Scaridae (parrotfish) and Acanthuridae (surgeonfish) families showed strong patterns of diel movement correlated with time of day and/or depth x time interaction (Table 2). Yellowtail parrotfish, stoplight parrotfish juveniles, and all damselfish, except bicolor and yellowtail, were significantly more abundant in shallow water throughout the day (Figure 4, 6, and 7; Table 1). Redband parrotfish were significantly more abundant in deep water (Figure 5; Table 1). Striped and princess parrotfish (including juveniles) was significantly hihger in shallow water in the morning. Abundance there decreased as the day progressed (Figures 8 and 9). Stoplight parrotfishwere significantly more abundant in the morning in deep water, but exhibited high abundances in the afternoon in shallow water and low abundances in deep water (Figure 10; Table 2). Striped and princess parrotfish showed the opposite pattern with decreasing abundance shallow in the morning and increasing abundance in deep water later in the day (Figure 9; Table 2) Ocean surgeonfish and blue tang per transect were most abundant in the morning; abundance decreased dramatically in the afternoon, except at 9.2 m, where abundances increased slightly (Figures 11 and 12; Table 2).

Complexity decreased significantly with depth ($F = 7.62$, $df = 1$, $P < 0.02$). The four transects differed significantly in substrate cover. Microalgae were significantly more abundant in shallow water than deep ($F = 42.52$, $df = 1$, $P < 0.000$), covering greater than 50% of the substrate, while macroalgae were significantly more abundant at depth than in shallow water ($F = 8.34$, $df = 1$, $P < 0.01$). Sand cover was absent at 1.5 and 4.6 m, present at 13.8 m, and comprising the majority of substrate at 9.2 m. The 13.8 m transect was mostly bare substrate. Coral cover did not vary significantly with depth ($F = 0.23$, $df = 1$, $P < 0.64$; Figure 13).

DISCUSSION

Evidence for partitioning of spatial resources in fish communities is equivocal (Abrams 1984, Talbot *et al* 1978). Some studies support the "lottery hypothesis" (Sale 1977; see also Sale 1982), which holds that diversity is maintained through stochastic variability in mortality and recruitment; other authors explain coexistence through niche partitioning and specialization (Anderson *et al* 1981). The Discovery Bay fore reef fish community shows clear evidence of spatial partitioning of resources. Nearly 65% of species analyzed showed distinction zonation with depth. The lack of consistent trends with depth within families

provides further support for partitioning. Fish within families should have more similar resource requirements, so that there may be more selective pressure for niche diversification and resource partitioning within families.

Table 1. Group of fish and ranked position within group at depth. "1" refers to most abundant, "4" refers to least abdundant. Common names are used for all fish. "Damselfish" refers to Threespot, Dusky, Cocoa, and Beaugregory as described in Methods. "*" indicates equal abundances. All df = 1.

Group	Depth (m) 1.5	4.6	9.2	13.8	F	P
Bluehead Wrasse Juveniles	1	2	3	4	52.8	0.0001
Bluehead Wrasse	1	2	3	4	5.2	0.020
Yellowhead Wrasse	4	3	2	1	40.0	0.0001
Yellowhead Wrasse Juveniles	3*	3*	1	2	5.5	0.025
Clown Wrasse	3*	3*	2	1	5.54	0.025
Creole Wrasse	3	2*	2*	1	8.3	0.007
Striped/Princess Parrotfish Juve-	1	2	4	3	31.1	0.0001
Yellowtail Parrotfish	1	2	3*	3*	9.42	0.005
Redband Parrotfish	4	3	1	2	27.6	0.0001
Stoplight Parrotfish Juveniles	2	1	3	4	7.2	0.011
Damselfish	1	2	3	4	79.9	0.0001
Yellowtail Damselfish	1	2	3	4	81.7	0.0001
Yellowtail Damselfish Juveniles	1	2	3*	3*	14.2	0.001
Harlequin Bass	4	3	2	1	31.6	0.0001
Barred Hamlet	4	3	2	1	23.8	0.0001
Shy Hamlet	3*	3*	2	1	18.79	0.0001
Yellow Goatfish	3*	3*	1	2	8.98	0.005
Surgeonfish	1	3*	2	3*	7.9	0.008
Blue Tang	1	2	3	4	15.1	0.001
Coney	2	3*	3*	1	13.8	0.001

Spatial partitioning of resources may be driven in turn by the partitioning of food resources. Four of five guilds showed strong relationships between depth and abundance; this suggests that gradients in food quality or availability affect zonation in fish abundance. Herbivores, for example, decreased with depth. This contrasts with the previously reported low abundances of herbivores near the reef crest, which has been linked to high surge (Russ 1984) and increased algal biomass and nutritional quality with depth (Steneck 1988, Bruggerman *et al* 1994). Atypical patterns at Discovery Bay may be related to increased algal biomass following the 1983 die-off of *Diadema antilarium*, the primary herbivore at shallow depths on the reef (Steneck 1988). Increased cover of highly palatable (Hickson 1996) filamentous microalgae observed in shallow transects support this proposition.

A significant proportion of the most abundant species of the fore reef fish showed evidence of diel movements. Active fishes as a group, and several members of the surgeonfish, parrotfish, and wrasse families all showed evidence of vertical migration (a significant main effect of time or depth x time interactions over the three days sampled). Changes in abundance appear to be related to diel movement rather than other factors which might cause spurious differences in abundance. Differences in activity might change detectability to a human observer and effect censuses. However, fish showing evidence of diel movement (with the possible exception of coneys) are diurnally active fishes which do not normally hide during the day. Moreover, individuals seen at periods of low abundance were still active (pers. obs.). The marked similarities in pattern of abundance within the family Acanthuridae (Figs. 11 and 12) and among parrotfish juveniles, adults and supermales (Figs. 8, 9 and Table 2), provide further support for the proposition that these patterns represent real diel movements.

Table 2. Diel movement as a function of time of day and time of day crossed with depth. "Shallow" refers to 1.5 and 4.6 m transects, "deep" refers to 9.2 and 13.8 m transects. All parrotfish supermales were only recorded at 1.5 and 4.6 m. All df = 2.

Group	Time F	Time x Depth F	Description
Parrotfish Supermales	7.85***	3.69*	High abundance at 1.5 m in AM, all abundance low rest of day
Striped Parrotfish Supermales	4.64**	5.65*	Highest abundance at 1.5 m in AM, all abundance low rest of day.
Striped / Princess Parrotfish	5.48***	2.14*	Highest abundance in morning at shallow depths, decreasing in PM.
Striped / Princess Juveniles	5.9***	3.55**	Highest abundance in morning at shallow depths, decreasing in PM.
Stoplight Parrotfish	2.86*	3.74**	High abundance deep, low abundance shallow in AM. High abundance shallow, low abundance deep in PM.
Yellowhead Wrasse	0.2*	3.9***	High abundance deep in AM, decreasing midday, increasing greatly in PM. Consistently low abundance shallow.
Damselfish	5.74***	3.25*	Highest abundance shallow, increasing throughout day.
Yellowtail Damselfish Juv.	3.7**	2.15*	Highest abundance shallow, increasing throughout day.
Surgeonfish	7.24***	4.5***	Highest abundance shallow in AM, all abundance low rest of day.
Blue Tang	12.3***	7.4***	Highest abundance shallow in AM, all abundance low rest of day.
Coney	0.60*	3.08***	High abundance deep in AM, decreasing midday, increasing greatly in PM. Consistently low abundance shallow.

* P > 0.05, ** P < 0.05, *** P < 0.01

The majority of species and groups which showed evidence of diel movement were most abundant at 1.5 m in the morning, and were less abundant as the day progressed (ocean surgeonfish, blue tang, princess and striped parrotfish, adults and juveniles, and all parrotfish supermales). All of these fishes are herbivores. If algal resources are superior in the shallow fore reef, this pattern of movement may function to allow herbivores to take advantage of algal resources when surge is lowest. Alternatively, parrotfish and surgeonfish might be responding to diel differences in territorial defense by herbivores. Damselfish defend territories which often contain superior algal resources (Beadell *et al* 1996). Damselfish abundance was greatest at 1.5 m, and increased from morning to evening. More abundant damselfish at shallow depths may reduce foraging efficiency of other herbivores in the afternoon and may cause them to migrate to other depths.

Diel patterns of stoplight parrotfish abundance provide the strongest evidence for clear-cut vertical migration (Fig. 9). Abundance increased throughout the day at the two shallow transects, and simultaneously decreased at the deeper transects. This could result from intraspecific interactions. Stoplight supermales often maintain territories in the zone of highest algal productivity (> 3.5 m in the Netherlands' Antilles, Bruggerman *et al* 1994), while other individuals forage over larger areas. If there is diel variation in intensity of territoriality, it might be advantageous for

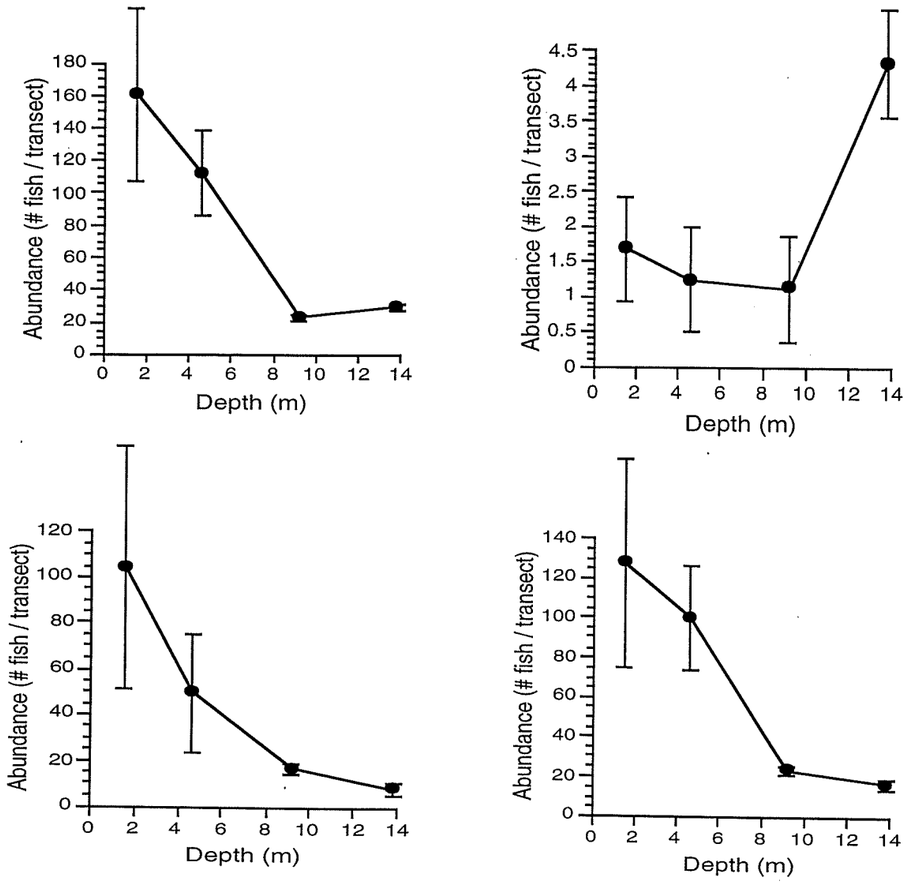

Fig. 1. Relative abundance of (a) herbivorous (upper left), (b) algivorous (lower left), (c) piscivorous (upper right), (d) invertivorous (lower right) fish as a function of time of day on the west fore reef at Discovery Bay, Jamaica

roving fish to forage in zones of peak density when defense is lowest. Another possible explanation is that stoplight parrotfish segregate sleeping and feeding areas, as has been shown for striped parrotfish (Ogden and Buckman 1973). Stoplight parrotfish sleep under boulders on the bottom, and may move up to 500 m during the day to feeding grounds (Bruggerman 1994). The upper reef, with increased structural complexity, may represent superior sleeping habitat, but stoplight parrotfish may leave shallow depths during the day because of patterns of resource availability, surge or displacement by other herbivores. Because our evening transect is closer to the day-night transition, increased abundance at 1.5 m in the evening may result from migration to shallow , sleeping areas

Diel movement may represent an alternate strategy for exploiting temporal partitioning of resources, and like depth zonation, may contribute to coexistence and the maintenance of diversity. Diel movement, especially vertical migration, also has implications for reef energetics and nutrient cycles. If a significant proportion of reef fish move regularly between reef zones, different portions of the reef may be energetically linked. French and white grunts are an important source of nutrients on the fore reef because they forage in the back reef at night and spend the day on the fore reef (Meyer and Schultz 1985). Diel movement may be especially important if fish migrate vertically because of depth gradients in primary

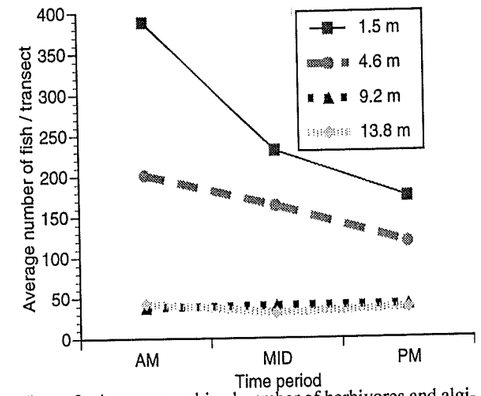

Figure 2. Average combined number of herbivores and algivores along four transects at four depths in the morning (AM), mid-day (MID), and late afternoon (PM) on the west fore reef, Discovery Bay, Jamaica.

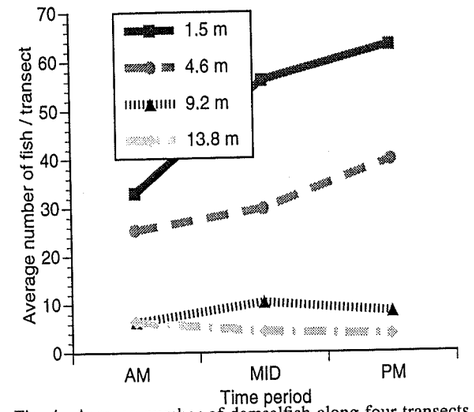

Fig. 4. Average number of damselfish along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

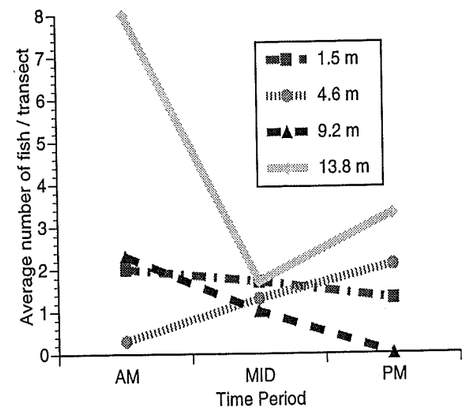

Figure 3. Average number of piscivores along four transects in the morning (AM), mid-day (MID), and late afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

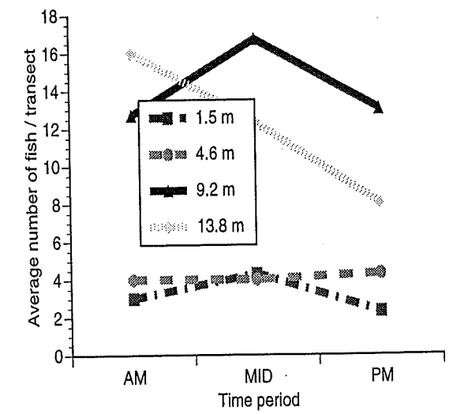

Fig. 5. Average number of red band parrotfish along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

productivity, nutrients and insulation. For example, a fish that feeds in one part of the reef and sleeps and excretes waste in another could have a substantial effect on reef energetics.

Vertical zonation of some fish species and guilds suggests that fish may partition spatial resources according to differential availability of food resources in different reef zones. Diel patterns of abundance suggest that some species may exploit these differences by showing predictable, cyclic movements. While these data offer tantalizing glimpses into diel movement of various fishes, the patterns are complex and cannot be explained from our limited observations. Further research should focus on patterns of diel movement in herbivores and should evaluate potential explanations for observed patterns. Future studies should examine fish movements across a greater range of horizontal and vertical habitat variation, with more frequent censuses for better resolution. Following tagged individuals may be necessary to discern exact patterns of movement. Because of the unusual disturbance history of Discovery Bay, the fore reef shows atypical depth gradients in physical structure and resource availability. Comparison of vertical zonation in fishes and their diel movements at Discovery Bay with those at other, healthier reefs may

Discovery Bay with those at other, healthier reefs may yield insight into mechanisms responsible for observed patterns in fish abundance.

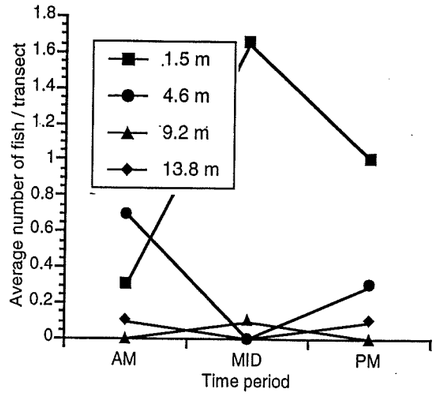

Fig. 6. Average number of yellowtail parrotfish along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

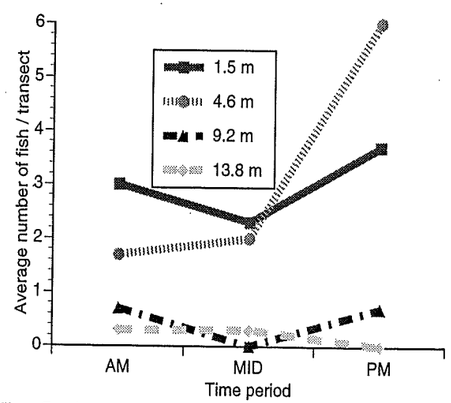

Fig. 7. Average number of stoplight parrotfish juveniles along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

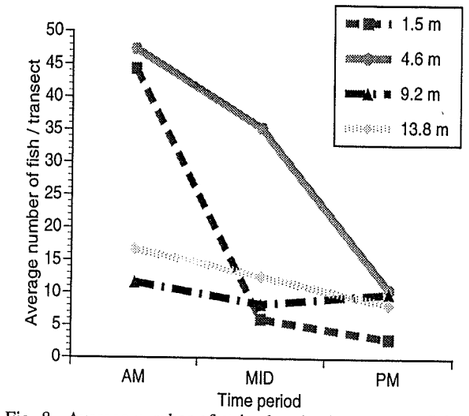

Fig. 8. Average number of striped and princess parrotfish-found along four transects at four depths in the morning (AM), mid-day (MID), and late afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

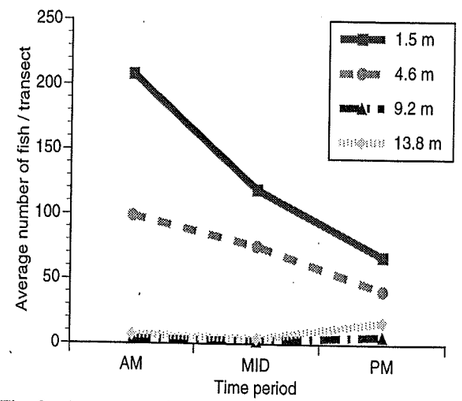

Fig. 9. Average number of striped and princess parrotfish juveniles along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

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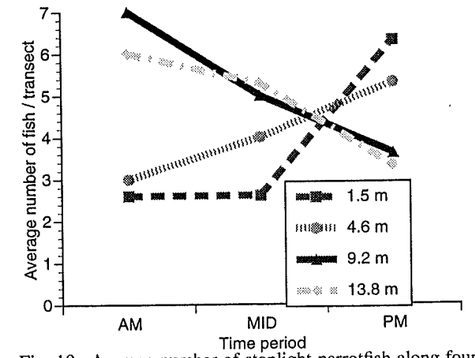

Fig. 10. Average number of stoplight parrotfish along four transects in the morning (AM), mid-day (MID), and later afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

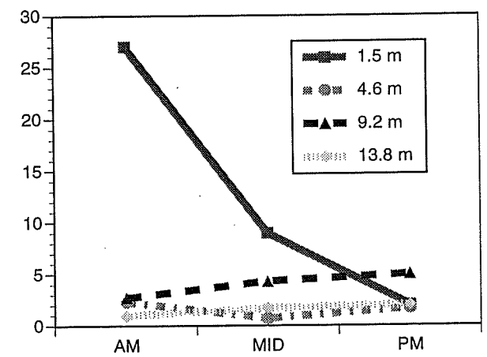

Fig. 11. Average number of ocean surgeonfish along four transects at four depths in the morning (AM), mid-day (MID), and late afternoon (PM) on the west fore reef at Discovery Bay, Jamaica.

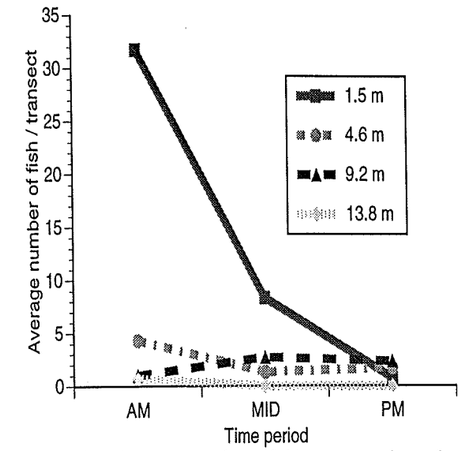

Figure 12. Average number of blue tangs along four transects in the morning (AM), mid-day (MID), and late afternoon (PM) on the west fore reef, Discovery Bay, Jamaica.

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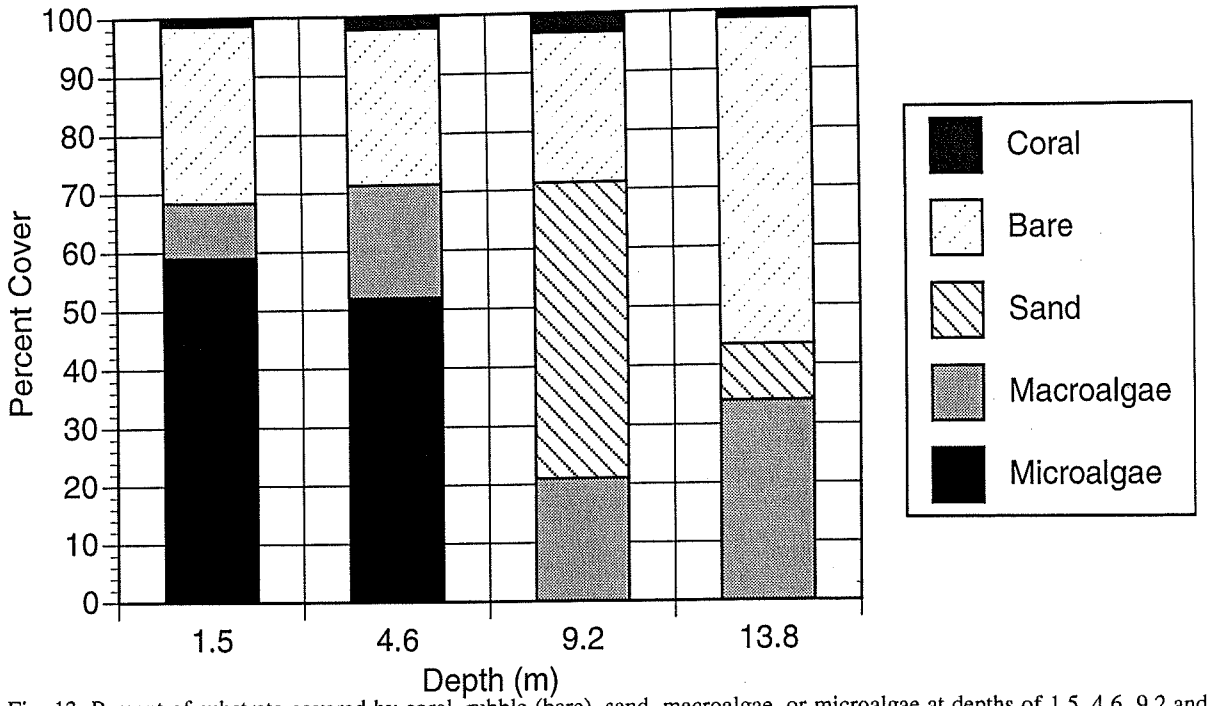

Fig. 13. Percent of substrate covered by coral, rubble (bare), sand, macroalgae, or microalgae at depths of 1.5, 4.6, 9.2 and 13.8 m on the west fore reef at Discovery Bay, Jamaica.

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Appendix. Common and Scientific names of species we observed 1 March - 8 March 1996 on the west fore reef, Discovery Bay, Jamaica.

Common Name	Scientific Name
Blue Tang	*Acanthurus coeruleas*
Ocean surgeonfish	*Acnthurus bahianus*
Coney	*Cephalopholis cruentata*
Bluehead Wrasse	*Thalassoma bifasciatum*
Creole Wrasse	*Clepticus parrai*
Yellowhead Wrasse	*Halichoeres garnoti*
Clown Wrasse	*Halichoeres maculipinna*
Shy Hamlet	*Hypoplectrus guttavarius*
Barred Hamlet	*Hypoplectrus puella*
Damselfish	*Stegastes* spp.
Yellowtail Damselfish	*Microspathodon chrysurus*
Yellow Goatfish	*Mulloidichthys martinicus*
Striped Parrotfish	*Scarus iserti*
Princess Parrotfish	*Scarus taeniopterus*
Harlequin Bass	*Serranus tigrinus*
Redband Parrotfish	*Sparisoma aurofrenatum*
Yellowtail Parrotfish	*Sparisoma rubripinne*
Stoplight Parrotfish	*Sparisoma viride*