

PATTERNS OF HABITAT PARTITIONING BY EIGHT
SPECIES OF TERRITORIAL CARIBBEAN DAMSELFISHES
(PISCES: POMACENTRIDAE)

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A B S T R A C T

Aspects of the habitat distributions of eight species of territorial Caribbean damselfishes of the genera *Eupomacentrus* and *Microspathodon* were examined at Puerto Rico and at Panama. Substrate and depth partitioning by various species was demonstrated with the use of transects in various reef and depth zones in Puerto Rico, although there was much multi-specific use of habitats. Habitats of exclusive usage were defined for some *Eupomacentrus* species in Panama and, in most, for certain size classes of the one species. Removal experiments suggest differences in the preference of different species for a given habitat. Habitat partitioning can account for the large-scale coexistence of most *Eupomacentrus* species. The coexistence of adult *Microspathodon chrysurus* and several *Eupomacentrus* spp. depends on the ability of *M. chrysurus* to aggressively dominate them and force them to share feeding areas with it.

Coral reefs harbor some of the most diverse fish assemblages known. Cohen (1970) estimated that some 8,000 species, or about 40% of all known living fishes, inhabit warm, coastal marine areas. Most of these species are associated with coral reefs. At least 1,000 to 1,250 species of coastal and shore fishes occur in the tropical western Atlantic (Robins, 1971). Böhlke and Chaplin (1968) list 507 species of fishes collected from in and around coral reefs in the Bahamas, while Starck (1968) recorded 517 fish species from Alligator Reef, Florida Keys. Even small patch reefs in the Caribbean may display an amazing diversity: Smith and Tyler (1972) found 75 fish species on one 3-m diameter reef in the Virgin Islands.

The factors which account for the maintenance of this high diversity on both small and large scales are not clearly understood. Explanations, which assume habitat saturation, tend to fall along a continuum which has the following two extremes. (1) Reef fishes are typically resource specialists and their resource requirements differ to the extent that interspecific competition is negligible or not severe enough to pose a problem for coexistence. (2) Many reef fishes are resource generalists. While more than one species is capable of realizing the same niche (thus constituting a guild, as defined by Root, 1967), environmental instability or chance factors involved in recruitment prevent any one species from excluding any other(s). Variations on this theme may incorporate interspecific differences in competitive abilities, or maintain that they do not exist.

There is considerable controversy regarding the importance of different mechanisms in allowing sets of apparently ecologically similar reef fishes to coexist on various scales. Russell et al. (1974), Sale (1974; 1975; 1976a; b; 1977; 1978a; b), and Sale and Dybdahl (1975; 1978) argue for the importance of generalization and opportunism in reef fish assemblages. Belk (1975), Risk (1972), and Smith and Tyler (1972; 1973a; b; 1975), among others, provide evidence of the importance of specialization and resource partitioning. Helfman (1978), Sale (1977), and Smith (1977) provide overviews of these arguments.

A group of ecologically similar pomacentrids in the genera *Eupomacentrus* and *Microspathodon* coexist on West Atlantic reefs. Both Clarke (1977) and Itzkowitz (1977) have demonstrated a degree of habitat partitioning among some of these

species, and characteristic associations of different Caribbean *Eupomacentrus* spp. with distinct habitat types have been described by other workers (Brawley and Adey, 1977; Itzkowitz, 1978; Kaufman, 1977; Williams, 1978). On the other hand, Emery (1968; 1973) found that all *Eupomacentrus* spp. and *M. chrysurus* inhabited more than one reef zone in his Florida Keys study areas, and that several species could be found in any one zone.

Here we document aspects of the patterns of association of seven territorial *Eupomacentrus* species and one *Microspathodon* with certain habitat types in two areas of the Caribbean Sea. We consider how these patterns of spatial distribution might have arisen and the possible contributions of resource partitioning, and generalization and opportunism, to the coexistence of these species on both large and small scales.

MATERIALS AND METHODS

The Species

The eight species of damselfishes we deal with here are the threespot damselfish, *Eupomacentrus planifrons*; the dusky damselfishes, *E. dorsopunicans* and *E. diencaeus*; the cocoa damselfish, *E. variabilis*; the beaugregory, *E. leucostictus*; the honey gregory, *E. mellis*; the bicolor damselfish, *E. partitus*; and the yellowtail damselfish, *Microspathodon chrysurus*.

All are territorial to some degree. All except *E. partitus* are essentially benthic-feeding fishes (Earle, 1972; Emery, 1968; 1973; Randall, 1967; DRR, observations on *E. diencaeus*). *Eupomacentrus partitus* commonly feeds both on the substrate and in midwater on plankton (Emery, 1973; Myrberg, 1972; Stevenson, 1972). Adults of the benthic-feeding *Eupomacentrus* spp. and *M. chrysurus* are intra- and interspecifically territorial (Brockmann, 1973; Ebersole, 1977; MacDonald, 1973; Myrberg, 1972; Myrberg and Thresher, 1974; Thresher, 1976), and defend essentially non-overlapping territories against each other.

Study Sites

Observations were made on reefs at two localities in the Caribbean Sea: at La Parguera off the southwest coast of Puerto Rico (by REW), and at San Blas Point in Panama (by DRR).

Observations in Puerto Rico were made between August 1976 and October 1978, and in Panama between March 1977 and October 1978.

Observations and Experiments

At Puerto Rico, data were collected on all but *E. diencaeus*, which was only seen at Panama. The work in Panama concentrated mainly on those species whose adults defend essentially non-overlapping territories against adults of other categories. While the substrate-feeding *Eupomacentrus* spp. in Panama are normally mutually territorial, a previously undescribed space-sharing relationship exists between several of these species and *Microspathodon chrysurus* (DRR et al., in prep.) which is briefly discussed below. No habitat distribution data were collected on *M. chrysurus* at that site. Most of the data on *E. mellis* were collected at Puerto Rico. This species is rare at the Panama site, where very few individuals exceed 30 mm total length.

Survey Procedures in Puerto Rico

The specificity shown by the study species for various substrates in Puerto Rico was examined by using strip transects. Thirteen 10-m \times 2-m transects were surveyed monthly from December 1976 through November 1977. The transects were distributed haphazardly on both inshore and offshore reefs, in areas considered typical of the La Parguera reef system. Transects ranged in depth from 1 m to 15 m, and averaged 5.5 m. Juvenile damselfishes were distinguished from adults by either (a) color pattern or (b) size in those species which do not change color at maturity. When sampling a transect, the substrate which a fish was within 15 cm of when first observed was recorded. When a fish was more than 15 cm from the substrate, the substrate in which it sought refuge when rapidly approached was noted. It is assumed that the results obtained by these methods reflect actual damselfish-substrate associations. The relative abundances of the substrates along each transect were determined by a technique similar to the chain-link method of Porter (1972). Two substrate diversity

measurements were taken within 10 cm of one another along the center of each transect, and the values obtained for each substrate were averaged. The numbers of damselfish of each species recorded as associating with each of the six most abundant substrate types were analyzed in three ways. (1) A 6×7 contingency table was used to determine if the observed distributions of the seven species could have been drawn at random from one population. (2) The substrate distribution of each size class of each species was compared with the distribution of each other size class of the same and each other species, using a chi-square test. (3) Using a chi-square test, the observed distribution of each species and size class over the six substrate types was compared to the distribution expected if the fish were randomly distributed over the substrates, given that the area of substrate sampled differed from one substrate type to the next. With these three analyses it was possible to determine whether all seven species showed a common distribution over the six substrate types which species differed significantly from which other species in its substrate distribution, and which species differed significantly from a random distribution over the six substrates.

In order to examine possible species differences in distribution over depth on the Puerto Rican reefs, 13 fore-reef and 8 back-reef transects, each 2 m wide, were made on two patch reefs (reefs less than 150 m in largest dimension) and on three shelf reefs that form part of the outer and inner barrier reef lines off La Parguera. Each transect was more than 15 m from any other. With this exception, the transects were haphazardly positioned on each reef. Except for the back-reef transects, all were divided into 3-m depth zones, and extended from the bottom of the reef slope to the reef crest. The back-reef transects extended only from 3 m depth to the reef crest, as previous examination of back-reef areas below 3 m revealed muddy back-reef slopes with little hard substrate and few pomacentrids. The damselfishes within each depth zone were recorded while swimming slowly over each transect. The length of each depth zone was estimated by counting the number of kicks necessary to swim across a zone parallel to the substrate and dividing this by the number of kicks used to swim a transect of known length. Surge and current were negligible during the sampling days and thus did not affect the accuracy of this method. In areas too shallow to swim, distances were visually estimated. The data on distributions over depth zones were analyzed by chi-square test in a manner similar to that used on the substrate utilization data.

Survey Procedures in Panama

Consistent differences in the distributions of six of the study species were examined by searching for habitat features with which members of only one species seemed to be associated. Subsequently, a series of eight habitats was defined and sampled over large areas by recording the numbers and approximate size of all damselfishes within each. Sizes were estimated based on the following criteria: Juvenile, $< \frac{1}{4}$ maximum mass of species; small, $\frac{1}{4}$ to $\frac{1}{2}$ maximum mass; medium, $\frac{1}{2}$ to $\frac{3}{4}$ maximum mass; large, $> \frac{3}{4}$ maximum mass, length/weight relations of each species having been previously determined. The eight habitats sampled were defined as follows: (1) Elkhorn fields and bluffs: Fields (Fig. 1A) consist of large expanses of coral and coral rock, with *Acropora palmata* comprising more than 90% of the living coral. The only other hard "coral" present in significant amounts is *Millepora*. Water depth ranges from 1 to 3 m. Fish counts were made in the centers of such fields; i.e., no closer than 10 m to their edges. Bluffs (Fig. 1B) are the tops of patches of living and dead *A. palmata* that are characteristically awash at low tide. They are found on the seaward, upper edges of patch reefs. Only fishes observed over live or dead *A. palmata* were counted on bluffs. (2) Staghorn thickets (Fig. 1C) are composed entirely of *Acropora cervicornis*. Water depth ranges from 1 to 5 m. The thickets sampled were all at least 2 m in diameter. (3) Shallow fore-reef *Agaricia* fields (Fig. 1D) consist of thickets of coral greater than 1 m in diameter that are composed chiefly of *Agaricia agaricites*, but also contain large amounts of *Millepora*. Water depth ranges from 2 to 5 m. These fields are found on the seaward side of sheltered patch reefs. (4) Deep back-reef *Agaricia* fields (Fig. 1E), which are composed almost entirely of *Agaricia* and its remains, are found on the leeward slopes of reefs situated on the leeward edge of San Blas Point. Water depth is from 5 to 15 m. In both these and the fore-reef *Agaricia* fields only fishes in the centers of the coral masses were counted; i.e., those within 25 cm of the edges were not included. This was done to avoid "edge effects" (see below). (5) Sandy slopes with boulders (Fig. 1F) occur in the same areas and depths as (4) above. The substrate is $> 75\%$ sand, with the remainder composed of scattered coral boulders (e.g., *Siderastrea*, *Montastrea*, *Diploria*) < 1 m in diameter, and barrel, tubular, and other noncryptic sponges. Masses of coral over 1 m in diameter and *Agaricia* clumps were not considered part of this habitat. (6) Sandy slopes with sponges (Fig. 1G) are found in the same general area as (5) above, and differ from it in lacking coral boulders and living corals. Water depth ranges from 3 to 15 m. (7) *Porites astreoides* back-reefs (Fig. 1H) are on the lee of patch reefs, and often shelve up to islands and beaches. Water depth is from 0.5 to 2 m. This habitat is characterized by an abundance of small, hemispherical coral heads (mostly *Porites astreoides*, but also *Siderastrea* and *Diploria*) and by a flat rock substrate. Fishes living in masses of branching coral (*Agaricia*, *Acropora*, *Porites* spp. other

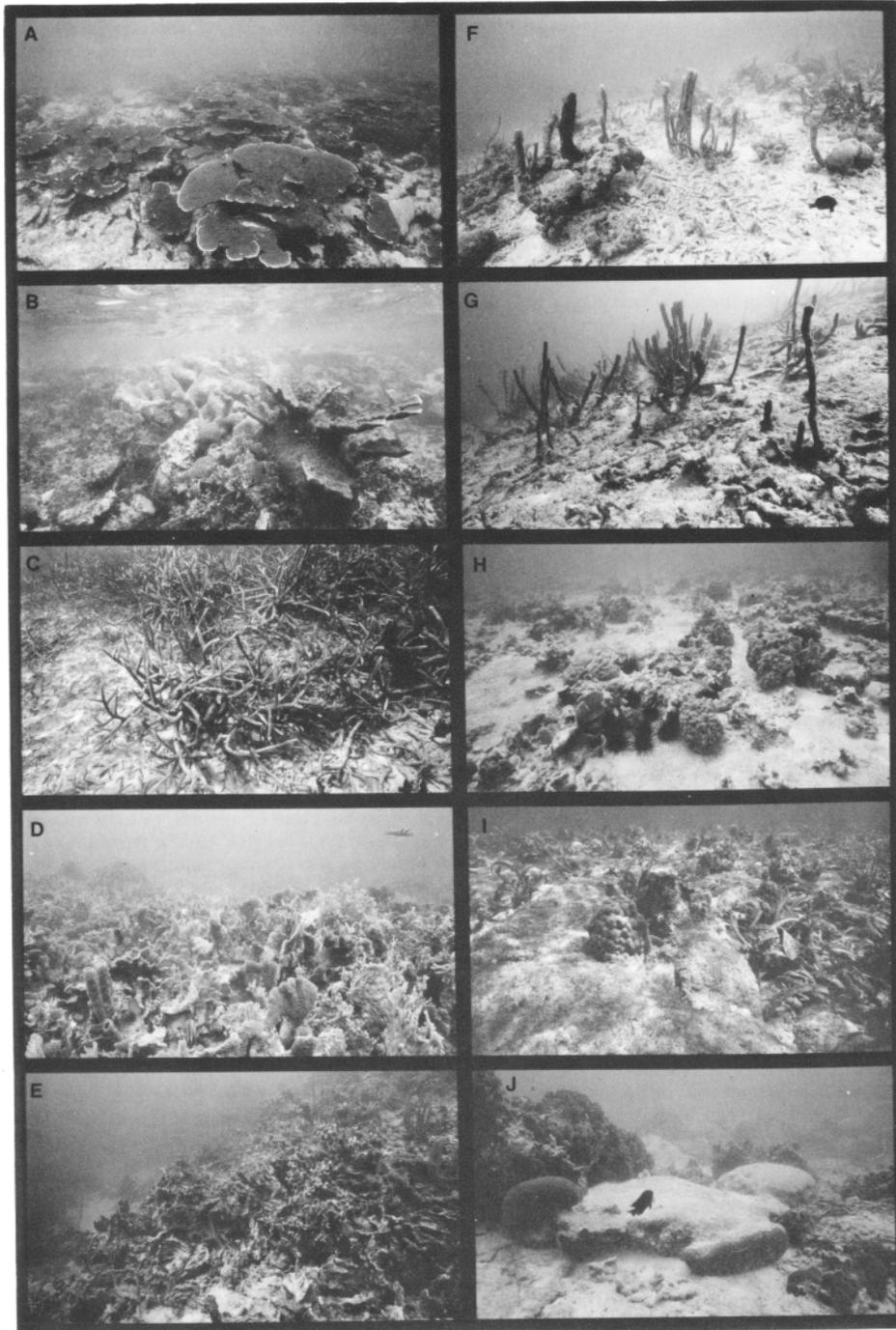


Figure 1. Panama habitat types (see Materials and Methods): A, Elkhorn Field; B, Elkhorn Bluff; C, Staghorn Field; D, Shallow Fore-Reef *Agaricia*; E, Deep Back-Reef *Agaricia*; F, Sandy Slope with Boulders; G, Sandy Slope with Sponges; H, *Porites astreoides* Back-Reef; I, Bare Back-Reef; J, Flat Rock Shelf with *Eupomacentrus diencaeus* resident.

than *P. astreoides*, and *Millepora*) more than 10 cm in diameter were not included in the counts, because large masses of such corals support a different damselfish fauna. (8) Bare back-reefs (Fig. 11) are found in the same general area as (7), and differ in (a) consisting mainly of low-profile, flat rock slabs that are half buried in sand, (b) having very few erect coral heads, and (c) in often having seagrasses mixed in with the pieces of hard substrate. This habitat is characteristically further from the main mass of a reef than is the *Porites astreoides* back-reef habitat. Water depth is between 0.5 and 2 m.

We emphasize that these eight habitats do not represent the full range of habitats present on the reefs of San Blas Point. However, all eight are common. There are over 150 reefs between 10 and 1,500 m in largest dimension spread over about 15 km² on the Point. All habitats except bare back-reefs and staghorn thickets are represented on 30–50% of those reefs, while the latter two habitats occur on about 20% and 10% of the reefs, respectively. On larger reefs the eight habitats frequently cover in excess of 1,000 to 10,000 m². Noncryptic sponges are extremely abundant on the back-reefs of reefs that lie along approximately 6 km of the leeward side of the Point. Shallow areas are common, with over 75% of the reefs having large areas that are awash at low tide. The sites sampled in this study were chosen haphazardly.

Observations in Overlap Habitat

In the habitat in which *E. variabilis* reaches its greatest relative abundance in Panama, two congeners are also common (Table 4). Observations on spatial distributions and agonistic interactions were made on a series of adult *E. variabilis* living in close proximity to members of the two other species in that habitat, to provide information on the potential for interspecific competition between them and the possibility of small-scale resource partitioning.

Experimental Procedures

A series of experiments aimed at testing the habitat specificity of *E. dorsopunicans* and *E. planifrons* was performed in Panama, by removing adults of *E. dorsopunicans* from areas immediately adjacent to large expanses of a habitat used by *E. planifrons*, and noting the identity of the individuals that replaced them. One series of *E. dorsopunicans* was removed (by spearing) from territories in elkhorn, at the junction of an elkhorn field and an extensive *Agaricia/Millepora* thicket occupied by *E. planifrons*. Another set of *E. dorsopunicans* was taken out of territories located on flattened coralline boulders and sand, contiguous with large fore-reef *Agaricia* patches used by *E. planifrons*.

RESULTS

Spatial Distribution Patterns

Puerto Rico Transects.—A total of 2,893 damselfish/substrate observations were made during the 12-month transect study, over half of which involved *E. planifrons* (Table 1). Few *Microspathodon chrysurus* juveniles, *E. variabilis* juveniles, or *E. leucostictus* were observed, probably due to the location of the transects and the relative abundance of each species on the reefs sampled. Monthly variation in total numbers was slight, and the overall diversity along the transects remained relatively stable throughout the sampling period (Table 2).

Table 1 shows the distribution of the seven species found in Puerto Rico on the six most abundant substrate types. Statistical analyses of these data strongly suggest differential substrate utilization, as follows: (1) The null hypothesis that the observed data could have been drawn at random from a single population was rejected ($P < 0.001$), indicating that differences in substrate utilization do occur among the study species. (2) All possible species and size class pairs showed significant differences in their substrate distributions with the exception of two pairs, *E. partitus* juveniles and *E. leucostictus*, and *E. dorsopunicans* juveniles and *E. mellis*. *Eupomacentrus partitus* adults and *E. variabilis*, *E. planifrons* juveniles and *E. variabilis*, and *E. dorsopunicans* adults and *M. chrysurus* differed at the 0.05 probability level; all other combinations differed at the 0.01 probability level. (3) The substrate distributions of all species and size classes

Table 1. Associations of seven species of damselfishes with six substrate types in the Puerto Rico transects

Fish		Percent of Fishes of Each Species on Each Substrate*						
Species	Size Class†	N	El.	St.	Ma.	Po.	Mi.	B.R.
<i>E. planifrons</i>	Juv.	391	3	18	66‡	6	6‡	1
	Adult	1,448	12‡	65‡	23	<1	<1	<1
<i>E. dorsopunicans</i>	Juv.	34	0	9	41	6	0	44‡
	Adult	337	12‡	19	54	1	4	10‡
<i>E. variabilis</i>	Total	56	4	12	84‡	0	0	0
<i>E. partitus</i>	Juv.	150	1	3	24	55‡	5	12‡
	Adult	344	<1	<1	25	65‡	4	6
<i>E. leucostictus</i>	Total	18	0	0	50	39‡	0	11
<i>E. mellis</i>	Total	40	0	0	30	13	0	57‡
<i>M. chrysurus</i>	Total	54	24‡	24	48	0	4	0
Percent of area of transects (260 m ²) represented by each substrate			4	29	48	11	2	6

* El. = elkhorn (*Acropora palmata*); St. = staghorn (*A. cervicornis*); Ma. = massive corals (e.g., *Monastrea annularis*); Po. = branching *Porites* sp. and its rubble <25 cm high; Mi. = *Millepora* spp; B.R. = beach rock.

† Juv. = juvenile (see Materials and Methods); total = juv. and adults when numbers are too small to permit separate analysis.

‡ Most-used substrates, determined on the basis of contribution to chi-square significance values (see Results).

differed significantly ($P < 0.01$) from what would be expected if random substrate utilization was occurring (except *E. leucostictus*, which differed significantly at the $P < 0.05$ level). It thus appears that the seven species studied in Puerto Rico generally differed in the substrates with which they most commonly were associated, although interspecific overlap in substrate use did occur.

The data from the fore-reef and back-reef transects show that there were differences in the overall distributions of the species over depth (Table 3; χ^2 ; $P < 0.001$). Significant differences in depth distribution ($P < 0.001$) were noted between all species pairs except *E. dorsopunicans* and *M. chrysurus*, and *E. planifrons* and *M. chrysurus*. All species differed in their depth distributions ($P < 0.001$) from what would be expected if random depth distribution was occurring,

Table 2. Number of damselfishes counted at monthly intervals on 13 Puerto Rico transects, December 1976–November 1977

Species	Month											
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
<i>M. chrysurus</i>	9	4	3	4	2	2	6	5	7	3	3	6
<i>E. partitus</i>	45	35	43	38	42	44	38	31	41	45	42	58
<i>E. planifrons</i>	136	135	162	149	143	161	164	155	158	155	166	158
<i>E. dorsopunicans</i>	34	38	34	34	30	30	34	29	41	27	21	27
<i>E. variabilis</i>	9	6	2	1	5	3	3	8	6	2	5	7
<i>E. leucostictus</i>	3	5	3	1	0	1	0	0	1	2	0	2
<i>E. mellis</i>	5	8	6	2	0	1	2	1	4	3	5	4
Total	241	231	253	229	222	242	247	229	258	237	242	262

Note: Differences in total numbers between Table 1 and Table 2 are due to some fishes associating with substrates other than those listed in Table 1.

Table 3. Density of six species of damselfishes in six depth zones on reefs at Puerto Rico*

Fish		Depth Zones					
Species	N	0-3 m	3-6 m	6-9 m	9-12 m	12-15 m	15-18 m
<i>E. planifrons</i>	568	0.19	0.36	0.25	0.15	0.01	0.00
<i>E. dorsopunicans</i>	220	0.11	0.10	0.08	0.02	0.00	0.01
<i>E. variabilis</i>	58	0.01	0.01	0.02	0.12	0.07	0.06
<i>E. leucostictus</i>	177	0.16	0.00	0.00	0.00	0.00	0.00
<i>E. partitus</i>	211	0.02	0.17	0.07	0.22	0.05	0.02
<i>M. chrysurus</i>	99	0.05	0.05	0.04	0.02	0.00	0.00
Percent of area of all transects (2,698 m ²) represented by each depth zone		41	26	11	6	9	6

* Data are based on 13 fore-reef and 8 back-reef transects. Back-reef transects were done at 0-3 m depth; fore-reef transects encompassed all depth zones present. Numbers are fish/m².

with the exception of *M. chrysurus*. Habitat partitioning by the species studied in Puerto Rico may thus involve several parameters, including substrate type and depth.

Panama Habitat Characterizations.—Consistent differences were found in the spatial distributions of six of the study species in Panama (Table 4). Three of the six species (*E. planifrons*, *E. dorsopunicans*, and *E. partitus*) had virtual exclusive occupancy of a habitat type. Such exclusivity could not be defined for *E. leucostictus* and *E. variabilis*. However, *E. leucostictus* did predominate in one habitat in which only one other species, *E. dorsopunicans*, was common. In the habitat in which *E. variabilis* reached its greatest relative abundance, only two other species were common, *E. partitus* and *E. planifrons* (*E. partitus* being the most abundant of the three).

A habitat of exclusive use could not be characterized for *E. diencaeus*. The few individuals observed during this study were only found in significant numbers on the outer edges of the back-reefs of reefs exposed to heavy wave action. In four such sites, 406 individuals were noted; 68% of those were associated with massive corals, such as *Siderastrea siderea* and *Montastrea annularis*, or large, horizontally flattened, dead coral formations (Fig. 1J), and 21% with small mas-

Table 4. Relative abundances of six *Eupomacentrus* species in eight habitat types in Panama

Species	Percentage of Total Fishes in Each Habitat Type* Represented by Each Species							
	El.	St.	S. Ag.	D. Ag.	S.B.	S.S.	P.B.P.	B.B.R.
<i>E. planifrons</i>	1.0	100	95.0	81.9	7.9	1.3	1.0	0.8
<i>E. dorsopunicans</i>	98.4	0	3.2	0	0.1	0.3	94.4	38.3
<i>E. variabilis</i>	0	0	0.1	10.5	14.3	2.8	0.7	2.3
<i>E. partitus</i>	0.4	0	1.7	7.6	77.6	95.4	2.8	6.0
<i>E. leucostictus</i>	0	0	0	0	0	0.2	0.6	53.4
<i>E. diencaeus</i>	0	0	0	0	0.1	0	0	0.1
<i>E. mellis</i>	0.2	0	0	0	0	<0.1	0.5	0
No. fish	2,085	1,439	2,562	620	5,937	1,726	2,013	2,308
No. sites	18	26	10	4	5	6	8	10

* Habitat types: El. = elkhorn fields; St. = staghorn thickets; S. Ag. = shallow fore-reef *Agaricia*; D. Ag. = deep back-reef *Agaricia*; S.B. = sandy slopes with boulders; S.S. = sandy slopes with sponges; P.B.P. = *Porites astreoides* back-reefs; B.B.R. = bare back-reefs. See Materials and Methods for descriptions.

Table 5. Size frequency distributions of five *Eupomacentrus* species present in eight habitats in Panama

Species	Size Class†	Percent of Fishes in Each Size Class in Each Habitat*							
		El.	St.	S. Ag.	D. Ag.	S.B.	S.S.	P.B.R.	B.B.R.
<i>E. planifrons</i>	J	70	2	35	27	70	96	100	100
	S	13	12	38	63	26	4	0	0
	M	17	27	22	10	4	0	0	0
	L	0	59	5	0	0	0	0	0
Sample size	(N)	23	1,439	2,521	508	470	22	20	19
<i>E. dorsopunicans</i>	J	10	0	10	0	25	60	53	84
	S	1	0	52	0	75	20	37	15
	M	25	0	38	0	0	20	9	1
	L	47	0	0	0	0	0	1	0
Sample size	(N)	2,049	0	85	0	4	5	1,928	884
<i>E. variabilis</i>	J	0	0	100	18	34	100	100	98
	S	0	0	0	48	34	0	0	2
	M	0	0	0	29	27	0	0	0
	L	0	0	0	5	5	0	0	0
Sample size	(N)	0	0	2	65	849	49	14	54
<i>E. partitus</i>	J	89	0	34	22	46	53	95	68
	S	11	0	37	46	35	26	5	28
	M	0	0	26	30	15	15	0	4
	L	0	0	3	2	4	6	0	0
Sample size	(N)	9	0	44	47	2,625	1,645	58	138
<i>E. leucostictus</i>	J	0	0	0	0	0	100	69	50
	S	0	0	0	0	0	0	23	28
	M	0	0	0	0	0	0	8	15
	L	0	0	0	0	0	0	0	7
Sample size	(N)	0	0	0	0	0	4	13	1,211

* Habitats: See Table 4.

† Size classes: J = juvenile; S = small, M = medium, L = large (see Materials and Methods).

sive corals on low-profile rock platforms. The remainder lived in immediately adjacent dead *Acropora cervicornis* rubble (3% of the fish) and *Agaricia* beds (8% of the fish). The only congener present in significant numbers in these habitats was *E. dorsopunicans*, which is morphologically very similar to *E. diencaeus* (Greenfield and Woods, 1974).

Table 5 shows the size-frequency distributions of the different damselfish species occupying the various habitats given in Table 4. Two species, *E. planifrons* and *E. dorsopunicans*, differ substantially in population structure in the different habitats in which they are abundant, suggesting segregation of their adults and juveniles by habitat. Three other species, *E. partitus*, *E. variabilis*, and *E. leucostictus*, have all size classes well represented in the habitat in which they are most abundant, and do not show such distinct habitat segregation. Further, in habitats used by more than one species, the population structures of those species differ. In most cases, the less abundant species are represented mainly by juveniles or small adults, while the more abundant species are represented by larger fishes.

Table 6. Summary of habitats that eight species of damselfishes are most characteristically associated with in various sites in the West Indies*

Species	Substrate or Habitat Type†	Depth Range
<i>E. planifrons</i>	Staghorn (1, 2, 4, 5, 6, 7), elkhorn (1), <i>Agaricia</i> (2), massive corals (1, 4, 5, 6, 8), <i>Millepora</i> (1)	Shallow–deep (1, 2, 9)
<i>E. dorsopunicans</i>	Elkhorn (1, 2, 6), beach rock (1), rocky back-reefs (2, 6)	Very shallow–moderate (1, 2, 8, 9)
<i>E. variabilis</i>	Back-reefs with sand and massive corals (1, 2, 8)	Moderate–deep (1, 2, 8, 9), shallow (9)
<i>E. leucostictus</i>	Bare back-reefs (2, 6), low-profile rubble (1)	Very shallow (1, 2, 8, 9), moderate (9)
<i>E. partitus</i>	Sandy slopes (1, 2), low-profile rubble (1, 2, 6, 8), beach rock (1)	Moderate–deep (1, 2, 8, 9), shallow (9)
<i>E. diencaeus</i>	Rocky back-reefs (2)	Very shallow–shallow (2)
<i>E. mellis</i>	Beach rock (1)	Very shallow (1), shallow–deep (8, 9)
<i>M. chrysurus</i>	Elkhorn and <i>Millepora</i> (1, 3, 6, 8, 9)	Very shallow–moderate (1, 3, 8, 9)

* Categorization of habitats by Emery (1973), Clarke (1977), and Itzkowitz (1977) differed in some respects from ours. This makes direct comparisons difficult in some cases.

† Authority: 1 = present study, Puerto Rico; 2 = present study, Panama; 3 = DRR unpublished observations; 4 = Williams, 1978 (Jamaica); 5 = Kaufman, 1977 (Jamaica); 6 = Itzkowitz, 1977 (Jamaica); 7 = Itzkowitz, 1978 (Jamaica); 8 = Clarke, 1977 (Bahamas); 9 = Emery, 1973 (Florida).

Concurrence of Data from the Two Sites.—The Panamanian and Puerto Rican data on spatial distribution patterns are summarized in Table 6, along with published data from other western Atlantic sites. They are in agreement in most cases. There are two apparent conflicts: First, in Puerto Rico *E. planifrons* greatly outnumbered *E. dorsopunicans* in elkhorn (Table 1), while in the Panama elkhorn sites *E. dorsopunicans* was virtually the only *Eupomacentrus* species present (Table 4). This difference, in part at least, is a reflection of differences in sampling techniques. In Panama, data were taken only in the centers of large, shallow elkhorn fields and on the tops of elkhorn bluffs, while all classes of elkhorn were included in the Puerto Rico data. *Eupomacentrus planifrons* is much more abundant in Panama around the deeper edges of elkhorn patches where those patches merge with other deeper substrates than it is in the shallow centers of those patches—*E. planifrons* constituted 16% to 34% of the *Eupomacentrus* spp. present in such edge elkhorn (N = 6 sites, 709 fishes in total), while it was virtually absent from the centers of those patches (Table 4). Similar edge effects probably operate in other habitat interfaces with other damselfish species.

Second, a substrate on which *E. partitus* is abundant in Puerto Rico—low, branching *Porites*—was not sampled in Panama. *Eupomacentrus dorsopunicans* is common in *Porites* in Panama, but not in Puerto Rico. However, the *Porites* sampled in Panama is *P. astreoides*, a nonbranching species, while the species sampled in Puerto Rico has a branching growth form.

Although substrate type may be one of the most important predictors of damselfish distributions, a particular substrate may support different species at different depths, or at sites with different degrees of exposure to wave action. For example, the abundance of *E. planifrons* relative to that of *E. dorsopunicans* on elkhorn increases with increasing depth in Panama. In Jamaica, *E. dorsopunicans*

occupies very shallow *Acropora cervicornis* beds while *E. planifrons* predominates in deeper stands of the same coral (Itzkowitz, 1977). A similar situation was observed in Panama and Puerto Rico, where *E. dorsopunicans* is abundant in *A. cervicornis* growing in very shallow, high wave-energy areas. Such *A. cervicornis* is rare at the Panama site (and was not included in the habitat counts referred to above).

Observations on Eupomacentrus spp. in Shared Habitat at Panama.—Observations were made on 35 adult *E. variabilis* (30 min/fish) living in the "sandy slopes with boulders" habitat. Those *E. variabilis* fed in areas ranging from 2 to 35 m² (\bar{x} = 13 m²). Thirty-two of the *E. variabilis* shared their large feeding areas with from 1 to 13 *E. partitus* (\bar{x} = 5.5 individuals), and 17 of the *E. variabilis* shared their feeding areas with 1 to 4 juvenile *E. planifrons*. A total of 177 *E. partitus* and 33 *E. planifrons* were resident in the *E. variabilis*' feeding areas. All of the *E. planifrons* and 175 of the *E. partitus* were smaller than the respective *E. variabilis* in whose area they lived.

Usually the *E. variabilis* were able to move freely about all over the substrate in the areas of the resident *E. partitus* and *E. planifrons*. Aggressive interactions between residents of the two species were infrequent and of low intensity. Only 22 interactions between 14 of the *E. variabilis* and 16 of the *E. partitus*, and seven interactions between five of the *E. variabilis* and seven of the *E. planifrons*, were seen. The *E. variabilis* invariably dominated (i.e., chased or displaced the other fish) when they had a size advantage, which they did in all except two interactions with two separate *E. partitus*. Those two *E. partitus* were the only individuals of either *E. partitus* or *E. planifrons* that were apparently excluding an *E. variabilis* from space inside the latter's feeding area. Each of the two was defending a small area around an apparent refuge.

Eupomacentrus variabilis adults also attacked and were attacked by *E. partitus* adults at the edge of the former's feeding areas. Twelve such interactions were observed, involving 7 of the 35 *E. variabilis* and 8 neighboring *E. partitus*. Five of these *E. partitus* were sexually active males (the sex of the remainder was not determined) that were defending nests, some of which contained eggs. Thus, much of the aggression directed by *E. partitus* at *E. variabilis* evidently represents the attempts of male *E. partitus* to defend their eggs, and perhaps, nest sites.

Table 7. Numbers of *Eupomacentrus dorsopunicans* and *E. planifrons* that took over territories from which *E. dorsopunicans* residents were removed in Panama

Habitat Type*	No. Fishes Removed	No. Times Replacement Fishes Were:			
		<i>E. dorsopunicans</i>		<i>E. planifrons</i>	
		Adult	Juvenile	Adult	Juvenile
Elkhorn at elkhorn/ <i>Agaricia</i> field junction	Adults	170			
	Juveniles	1	167 0	7 1	4 0
	Total	171(42)†	175		6
Coral rock and sand contiguous with <i>Agaricia</i> field	Adults	14(14)†	12	1	1 0

* See Materials and Methods for description of habitat types.

† Numbers in parentheses refer to numbers of territories from which (often successive) removals were made.

Removal Experiments.—The Panama experiments (Table 7) show that, in habitats used virtually exclusively by *E. dorsopunicans*, conspecifics almost always recolonize territories whose owners are removed, even where *E. planifrons* probably are close enough to be able to detect the occurrence of vacancies. These vacated territories were taken over rapidly by new fishes; 27 of 28 of the elkhorn-series territories had been completely taken over the day following removal of the original occupant. All 14 of the second-series territories were being defended by new fishes within 3 h of the removal of the owner. Most territories remained occupied, despite repeated removals (up to six removals in 3 weeks in each territory), although four of the 42 elkhorn-series territories remained empty for at least 1 day. The new residents were normally smaller [by $\bar{x} = 3 \pm 1$ mm (95% C.L.) S.L., N = 41] than the previous occupant(s).

DISCUSSION

Patterns of Spatial Distribution and Their Causes

Our data demonstrate the existence of greater interspecific habitat partitioning among the *Eupomacentrus* species than has previously been described. Along with previously published data, our results show that a species is often associated with the same type(s) of habitat in widely separated points in the West Indies. Habitat segregation of conspecific juveniles and adults is also evident in some species. In others, juveniles are common in both the same habitat(s) in which their adults are concentrated and habitat(s) in which their adults are rare (Clarke, 1977; Itzkowitz, 1977; Williams, 1978). Although our two sets of data do not show the same degree of interspecific habitat segregation, the data are complementary rather than contradictory. While there is multispecific use of many habitats, other habitats that are used virtually exclusively by single species also exist. The latter require precise definition in terms of water depth, location on a reef, and substrate type, including coral species or growth form, and density of living or dead coral.

These differences in patterns of distribution could be the result of differences in the ecological requirements and habitat preferences of different species (and different size classes of the same species), differences in the competitive abilities of different species or size classes, or some combination of the two. Itzkowitz (1977) has suggested that such differences are due to differential mortality of juveniles of each species in different habitats. Few experiments have been conducted to test the roles of these possible effects on distribution. Williams (1978) provides suggestive evidence of competitive exclusion of *E. dorsopunicans* by *E. planifrons* in some areas, with *E. planifrons* adults also excluding conspecific juveniles. When considered in this context, the results of the Panama experiments may indicate that the habitat in which *E. dorsopunicans* replace conspecifics represents nonpreferred habitat for all size classes of *E. planifrons*. Alternatively, it may be nonpreferred habitat for only certain size classes of the latter species. In many fishes, including damselfishes, a size advantage often appears to enable one fish to aggressively dominate both conspecifics (Myrberg, 1972; Itzkowitz, 1977; 1978), and congeners (Itzkowitz, 1977). Among damselfishes, size differences seem to correlate with and may determine priority of access to space in the field (Clark, 1970; Williams, 1978). The Panama removal experiments suggest a similar size advantage with *E. dorsopunicans*. The dominance relationship between *E. planifrons* and *E. dorsopunicans* suggested by Williams (1978) may be size rather than species specific, because the *E. planifrons* were bigger than the *E. dorsopunicans* in her removal experiments. Since *E. dorsopunicans* is much smaller than *E. planifrons* in Panama, size-dependent dominance relations may

be affecting the distribution of these two species there. Indeed, the absence of small *E. planifrons* from "elkhorn fields" in Panama could be due to their being excluded by larger *E. dorsopunicans*.

Despite this lack of experimental evidence, it seems to us that the distinct interspecific habitat segregation of larger adults of most *Eupomacentrus* species in Panama is the result of each preferring a different habitat type and having little "interest" in that occupied solely by large adults of other species. Of the species studied, only *E. diencaeus* does not clearly fit this pattern. The literature contains evidence of interspecific differences in (1) maximum size (Emery, 1973), which probably results in differences in shelter requirements (Smith and Tyler, 1972; 1975); (2) diets (Emery, 1973; Randall, 1967); and (3) the way fishes use and defend space (Thresher, 1977), which are in accord with this type of segregation.

There is, nonetheless, much sharing of certain habitats by various combinations of species. There are relatively few species of damselfishes in the Caribbean (Emery and Burgess, 1974), and reefs are structurally complex and variable, containing many intergrading and intermingling habitat elements. These fishes are evidently sufficiently generalized that many areas supply the requirements of more than one species. While the occupancy of sites in overlap habitats may be influenced by opportunism, much as Sale (1974 and later papers) has hypothesized, both interspecific changes in occupancy of sites in such habitats and a lack of such change in exclusive-use habitats could also be the result of members of competitively more dominant species (or size classes) simply not being present to fill vacancies. Dale (1978) hypothesizes that, for many reef fishes, a species' recruits often colonize both preferred and nonpreferred habitat, and that different processes determine the numbers of species present in different habitats. His model stresses the importance of refuge habitats to species that co-occur and interact competitively in other habitats. Our data can also be fitted to this hypothesis.

Discussions of ecological interactions between and within species of reef fishes have tended to consider reef fish populations to be at levels at which space is saturated. However, critical testing of the possibility that various resources, and especially space, are available in a surplus has barely begun. The results of the removal experiments, which show that vacated areas are rapidly filled by adults rather than newly settled larvae, support the notion that space is saturated in some areas or habitats, and that there is intraspecific competition for it. Alternatively, the previous owner(s) of a vacated site may have improved its quality, by using and defending it (e.g., the formation of algal mats by *E. planifrons*; Brawley and Adey, 1977; Kaufman, 1977) to the extent that it may be cheaper for a fish to move into a previously occupied site rather than to either continue in a newly occupied one or set up a new territory in a "virgin" area. Such behavior might maintain fish densities at about the same level for some time, in a small area, in the presence of a surplus of potentially usable unconditioned space.

In this regard, it is interesting that there were large expanses of seemingly suitable habitat in 10 to 20 m of water in both of our study areas in which the study species were present in low densities (see also Brawley and Adey, 1977). Studies by one of us (DRR et al., in preparation) show that, even in more densely populated shallow areas, *E. planifrons*' population density can be increased experimentally. This indicates that a surplus of potentially usable space exists even in some high-density areas. One consequence of such surpluses of space might be increased multispecific occupancy of habitats due to reduced intensity of interspecific competitive interactions.

Large-Scale Coexistence of the Study Species

Habitat partitioning is sufficiently distinct that the persistence of at least three species (*E. planifrons*, *E. dorsopunicans*, and *E. partitus*) can be attributed to each having a habitat refuge. Each of the four remaining *Eupomacentrus* spp. shares the habitat with which it is most characteristically associated with at least one congener. We will consider each of these species in turn, and also the relationship between *M. chrysurus* and some *Eupomacentrus* spp.

Eupomacentrus variabilis.—In Panama, *E. variabilis* shares “sandy slopes with boulders” with *E. partitus* and *E. planifrons* (Table 4). Such *E. partitus* and *E. variabilis* often share feeding space there rather than defending exclusive territories against each other. *Eupomacentrus variabilis* reaches a greater absolute size than *E. partitus* in that habitat, and individual *E. variabilis* are aggressively dominant when they have a size advantage over the *E. partitus* (except perhaps brooding *E. partitus* males). We therefore suggest that competition between these two species is very weak in this habitat, and that *E. variabilis*' size advantage gives it a competitive advantage over *E. partitus*. Differences between the feeding habits of *E. variabilis* and *E. partitus* and differences in their shelter needs that arise from differences in their sizes may account for the weakness of the competitive interaction.

Eupomacentrus planifrons is about half as abundant as *E. variabilis* in the latter's habitat and, while most of the *E. planifrons* there are juveniles, the larger size classes of *E. variabilis* are well represented. Because *E. variabilis* adults often share their feeding areas with, and aggressively dominate, smaller *E. planifrons* juveniles, it seems unlikely that competition for space with *E. planifrons* represents a serious problem for *E. variabilis* in that habitat. Competitive interactions between the most abundant size classes of each species seem weak, and *E. variabilis* seems to be dominant in such interactions.

Eupomacentrus leucostictus.—One other species, *E. dorsopunicans*, is abundant in the *E. leucostictus*' habitat. The population structures of these two species are different in this habitat (χ^2 , $P < 0.001$); while adult *E. leucostictus*, including larger adults, are common, the great majority of the *E. dorsopunicans* are juveniles, and the few adults present are small. Thus the larger size classes of *E. leucostictus* have a habitat refuge. Clarke (1977) also refers to a possible habitat refuge for *E. leucostictus*. Interactions between the juveniles of these two species require further examination.

Eupomacentrus diencaeus.—There are no indications that *E. diencaeus* has a habitat refuge in Panama. Its interactions there with *E. dorsopunicans*, a far more abundant species that evidently has more generalized habitat requirements, require further work to elucidate the mechanism(s) of their coexistence. *Eupomacentrus diencaeus* may have some competitive advantage since it reaches over twice the mass of *E. dorsopunicans* in Panama (60 g versus 25 g) and is a highly aggressive species.

Greenfield and Woods (1974) found that *E. diencaeus* and *E. dorsopunicans* live in different habitats in Belize, and that “in no case were the two species found occurring in the same area.” Thus *E. diencaeus* apparently does have a habitat refuge in part of its geographic range. How this habitat segregation is brought about in Belize, and whether this species' persistence in San Blas is achieved by the same mechanism, remains to be shown.

Eupomacentrus mellis.—There are no indications that *E. mellis* has a habitat refuge in either Panama or Puerto Rico. Resource partitioning cannot therefore be invoked to explain its persistence at these sites. As it is smaller, as an adult,

than all the other benthic-feeding *Eupomacentrus* (Emery, 1973; Emery and Burgess, 1974), there are no obvious features that might give it a competitive advantage.

There is a possibility that *E. mellis* is a hybrid. Although Rivas (1960) considered it to be such, Emery and Burgess (1974) described it as a valid species. Two more recent sets of data support the hybrid hypothesis: First, no mature females have been found in collections made by REW of 103 specimens taken over one year at Puerto Rico, or by other workers in other areas (R. D. Clarke and A. R. Emery, pers. comms. to REW). Second, *E. mellis* shares a dactylogyrid monogenetic trematode with *E. dorsopunicans* (Waldner and Williams, 1978; Williams and Waldner, in prep.), and this group of parasites are extremely host-specific (Shulman, 1958). If *E. mellis* is eventually shown to be a hybrid, its persistence presents less of a problem than it would if it is a valid species.

One of the reviewers of this paper pointed out that recent, unpublished, electrophoretic studies indicate that *E. mellis* is not intermediate between any other Caribbean *Eupomacentrus* spp., and may therefore be a valid species. According to Emery and Burgess (1974) it is most abundant in clear-water areas around islands. If it is a valid species, the reasons for its rarity in our study areas require investigation. Our somewhat "continental" study sites may not contain its optimal habitat, or it may be outcompeted at them.

Microspathodon chrysurus.—*Microspathodon chrysurus* reaches its greatest abundance in habitats occupied by *E. dorsopunicans* and, to a lesser extent, *E. planifrons* (Clarke, 1977; Emery, 1973; Itzkowitz, 1977; and our Puerto Rico data). The relationship between *M. chrysurus* and these two *Eupomacentrus* spp. at Panama has been under study for some time (DRR et al., in prep.). Individuals of *M. chrysurus* and these two *Eupomacentrus* spp. characteristically cohabit space, rather than defending mutually exclusive territories in Panama. While all three species are intraspecifically territorial, the feeding areas and territories of *M. chrysurus* are normally superimposed on those of significantly smaller members of the two *Eupomacentrus* spp. The territories of the largest *M. chrysurus* cover those of *E. dorsopunicans* of all sizes. Large *M. chrysurus* have a similar relationship with *E. planifrons*, but superimpose their territories only on those of *E. planifrons* that are less than about half *E. planifrons*' maximum size. *Microspathodon chrysurus* attains six times the mass of *E. dorsopunicans* and three times that of *E. planifrons*. This size advantage apparently enables it to dominate the smaller *Eupomacentrus* spp. and feed in their feeding areas, although large *E. planifrons* are able to successfully exclude all *M. chrysurus*. There is a great deal of similarity in the diets of *M. chrysurus* and its cohabitant *E. dorsopunicans* in Panama, and in their feeding microhabitats. *Microspathodon chrysurus* thus seems to be able to persist as a species in Panama not because of resource partitioning, but because the *Eupomacentrus* spp. cannot exclude its large juveniles and adults. The relationship between small juveniles of these three species is still being investigated.

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