

## SPATIAL DISTRIBUTION PATTERNS AND COEXISTENCE OF A GROUP OF TERRITORIAL DAMSELFISHES FROM THE GREAT BARRIER REEF

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### A B S T R A C T

To test a hypothesis that resource partitioning is less important to the small- and large-scale coexistence of similar species of reef fishes than are the chance elements involved in patterns of mortality, recruitment, and space-creation, the patterns of spatial distribution of a set of damselfishes were examined on both large and small scales. The data show a greater degree of within and between habitat segregation than was previously thought to exist. Space partitioning is thus of significance to large- and small-scale coexistence in many cases. While the "chance" hypothesis remains relevant to those cases in which resource partitioning is not evident among actively competing species, the existing data also fit alternative, more conventional hypotheses. Competitively interacting species may also differ in the extent to which their populations are space limited and reliant on external agencies to create new space.

In a series of papers that has stimulated considerable discussion among reef fish biologists, P. F. Sale has developed and promoted a new hypothesis to account for the continued coexistence of groups of ecologically similar species of coral reef fishes, and hence the maintenance of high species diversity in reef environments (Sale, 1974; 1975; 1976a; b; 1977; 1978a; b; Sale and Dybdahl, 1975; 1978). As is explained in his 1977 paper, this hypothesis represents a different alternative to the more classical view that coexistence results from a high degree of specialization of different species, i.e., each species has a specific set of abilities that give it competitive superiority over all others in at least one situation, so that it has a refuge from which it cannot be competitively excluded. Specialization is often thought to reduce the intensity of, or preclude, interspecific competition. Sale's "lottery" hypothesis maintains that many species of reef fishes are not specialized, but have ecological requirements and abilities that are essentially the same as those of other species, and that the local coexistence of such species, which are actively competing, results from chance determining which species occupies vacant space. The purpose of this paper is to examine aspects of Sale's hypothesis and to present additional, pertinent data.

Sale initially developed his hypothesis to account for the coexistence of a group of species of damselfishes (Pomacentridae) that defend permanent, general purpose territories (Sale, 1974). We concern ourselves with this same group, which Sale considers to represent a guild (*sensu* Root, 1967). As we understand it, there are six parts to the lottery hypothesis: (1) Competition for space (which is in short supply and limiting) is an ongoing process both within and between many species of reef fishes. Data base: (a) At least three species of one guild are both intra- and interspecifically territorial towards each other. (b) Territory vacancies that are experimentally created are rapidly refilled. (c) The overall proportion of the space in an area that is occupied by such species remains fairly constant over extended periods of time. (2) Guilds of species, which have essentially the same requirements for space and abilities to compete for space, are common among reef fishes. Habitat partitioning by such species is not an important mechanism by which their small-scale coexistence is achieved. Data base: (a) There are broad

overlaps in the zonal distributions of guild members; in some cases the data show complete overlaps. (b) No evidence was found of substrate partitioning by three species in one zone in which they co-occur. (c) In small areas inhabited by three species of territorial damselfishes, specific sites were used by different species at different times and, when a change in occupancy occurred, which species took over a site was not related to which species previously held the site. (iv) These same three species defend space against each other, as well as intraspecifically. (3) Prior residence is of overriding importance in determining the outcome of intra- and interspecific competitive interactions for space. Data base: (a) Literature that discusses the advantage resident fishes have over nonresidents in aggressive interactions is cited. (b) Different species of damselfishes defend relatively exclusive territories against each other. (4) New spaces, suitable for more than one guild species, are being continually created although when and where such spaces are created is unpredictable. This creation of vacant space is the result of physical disturbance (storms and cyclones) and the mortality or departure of resident fishes. It is implied that the process of opening up of new space is beyond the control of these fishes. Data base: (a) Most of these territorial damselfishes live in association with substrates composed of dead coralline rock and rubble. These substrates support the algae and other benthic organisms on which they feed. (b) Storms and cyclones often destroy areas of living coral on the study reef. (c) Damselfishes die of disease and predation. (5) From the point of view of their parents, where and when planktonic larvae of various species settle is unpredictable. Data base: These and many other species of reef fishes have planktonic larvae. They also have extended breeding seasons during which larvae are produced in large numbers. (6) Chance determines which species arrives first at a suitable vacant site on the substrate. Because of the effect of prior residence (3 above), the first fish at a site claims it. Some species may have a better chance of arriving first at vacated sites because they recruit at higher rates. This advantage is offset by their suffering higher rates of mortality. Data base: One of three species of interacting damselfishes that recruits at higher rates than the other two also appears to have a higher mortality rate (among postlarval fishes).

There are two questions concerning how the coexistence of similar species is brought about: (1) By what mechanisms does each of a pool of species persist on a large scale (on a reef as a whole, for example)? (2) By what mechanisms do a number of such species coexist in relatively small areas—the same zone or general habitat type? Sale's data and discussions relate primarily to local coexistence. Here we deal with both questions since they may or may not have the same answers and because we wish to examine the relevance of the lottery hypothesis to both of them.

One of the most interesting parts of this hypothesis concerns the importance of the degree of similarity of the guild species. Sale concluded that individuals of the different species were essentially the same in terms of their requirements for space and abilities to compete for space in his study area. This conclusion follows from his finding very high degrees of overlap in spatial distributions of various species.

We decided to test this idea of interspecific similarity and lack of importance of differences in ecological requirements and competitive abilities by considering it in the following way. If the habitat requirements and ability to use different habitat types of each of a set of species are essentially the same, we should not be able to find evidence of well-defined habitat segregation, and especially of such segregation in areas in which the zonal distributions of different species

overlap. If, however, we can demonstrate such habitat segregation, then the coexistence of such a group of species on both large and small scales is more amenable to explanation by various conventional hypotheses, including the specialization hypothesis, than was previously thought. We therefore made a more extensive examination of the patterns of spatial distribution of the five species to which Sale originally devoted most attention (Sale, 1974).

The data that we present deal almost entirely with spatial distribution patterns. However, on the basis of observations by one of us (D.R.R.) on both Heron Reef and Caribbean reefs, we will discuss other parts of Sale's hypothesis. We shall also consider how his data are consistent with more conventional hypotheses and attempt to combine parts of the lottery hypothesis with these hypotheses.

## MATERIALS AND METHODS

### Study Area

The observations on the spatial distribution patterns of the six species of damselfishes were made on Heron Reef, on Australia's Great Barrier Reef, the same site on which Sale studied those species. The data presented here were collected during November 1977.

### Species Studied

Damselfish nomenclature is at present in a quite fluid state. Here we follow the names used by Sale (1977) and Allen (1975). Sale's original (1974) paper (and most of his subsequent papers) deals principally with *Pomacentrus wardi*, *Eupomacentrus apicalis*, and *Plectroglyphidodon lacrymatus*, and to a lesser extent with *Pomacentrus flavicauda* and *Glyphidodontops biocellatus*. Besides examining these five species, we also collected data on the spatial distributions of one other species that Sale described as a guild member—*Pomacentrus bankanensis*. The approximate maximum sizes that each of these six species reach in the study area are shown in Table 1. Sale has pointed out that the species differ in their sizes. However, while he used length as a measure of size, we use mass, as it is a better indicator of differences. Unless stated otherwise, our use of the term "guild species/members" in this paper refers to these six species alone.

### Spatial Distribution Data

Sale examined patterns of spatial distribution in three ways. First, counts were made of the different species along two vertical transects that were run across the southern side of Heron Reef. Second, the distributions of *Po. wardi*, *P. lacrymatus*, and *E. apicalis* were compared with the distributions of three substrate types along three 99-m-long transects that were run horizontally along the subtidal reef slope. Third, the use of space by these same three species was studied in four small areas on the upper reef slope. A series of short-term observations was made at intervals of several months over a period of several years.

We collected two types of data.

*Transects.*—Heron Reef is quite large and Sale examined only a small portion of it on its south side (Fig. 1). We made seven sets of transects to obtain data on the zonal distributions of the six species, four in the same general area as Sale's (1974) two transects, and three on the opposite side of Heron Island (Fig. 1). This number of transects would, we thought, enable us to determine to what extent zonal distribution patterns might be repeated over a relatively large section of Heron Reef and to what extent they might be repeated on two different sections.

Rather than being simple line transects (such as Sale used), each of our seven transect sets comprised a series of small transects running perpendicular to a main transect line that ran from the edge of the island out to the reef edge. These subtransects sampled major substrate zones that differed from one another in terms of their physical structure. On the south side of Heron Reef, six such zones were sampled (Fig. 2): (a) *beachrock edge*, the seaward extremity of the beachrock platform that ran along the outer edge of the beach. (b) *inner moat edge*, to seaward of the beachrock a shallow moat (that contained virtually no cover for substrate-living damselfishes) is present. Subtransects were run at the seaward edge of this moat where coral cover started to appear. Much of the shelter in this area is quite sparsely scattered and of low relief (flat rock slabs imbedded in sand). (c) *reef flat*, this comprises areas of scattered coralline rock and coral on sand and rubble. (d) the *reef crest* consists of a compacted coralline rock pavement with scattered, very low, encrusting coral growth, often with

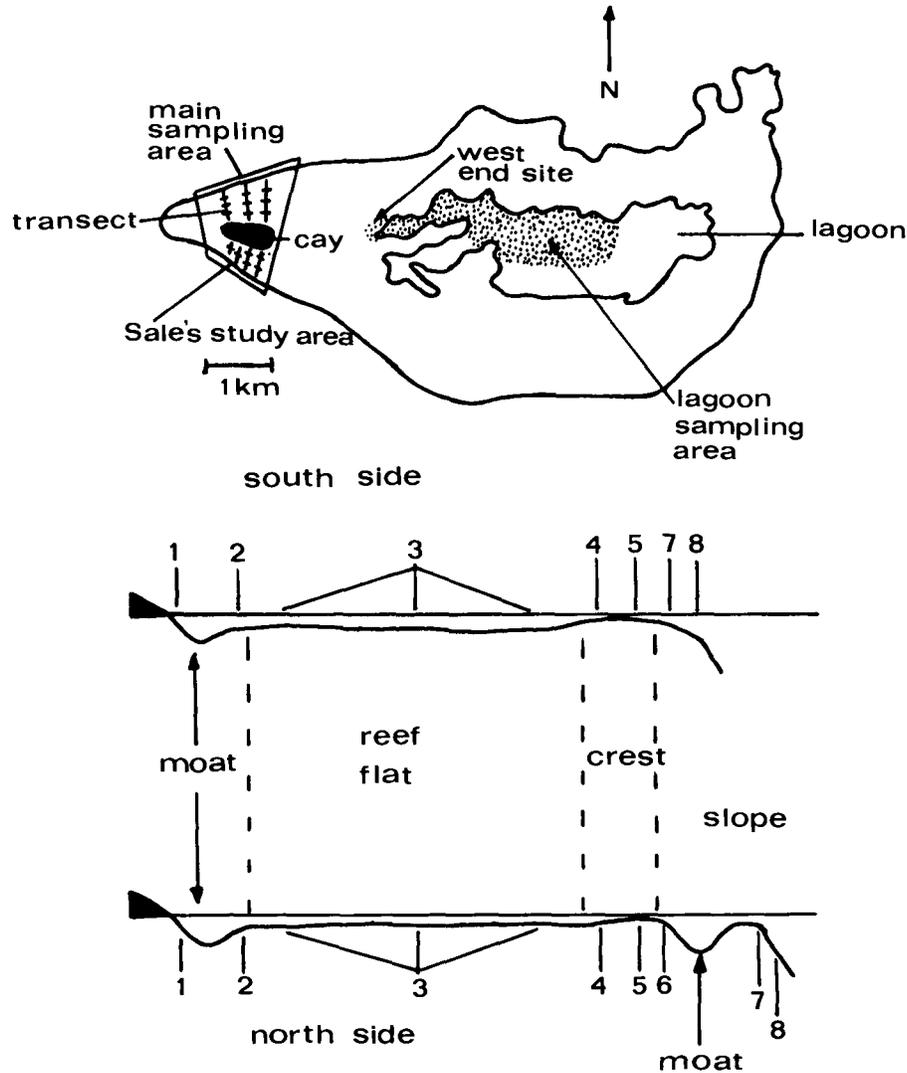


Figure 1. (Upper) Heron Reef showing sampling areas used in the present study and the general location of Sale's study area. Figure 2. (Lower) Location of transects in different zones on the north and south sides of Heron Reef: 1, Beachrock; 2, Moat Edge; 3, Reef Flat; 4, Inner Reef Crest; 5, Outer Reef Crest; 6, Inner Lip; 7, Outer Lip; 8, Upper Reef Slope.

rubble and boulders on its inshore side. On the north side of the island the reef crest is much wider and more rubble covered than that on the south side. (e) the *outer lip* is the transition point between the intertidal reef crest and the subtidal reef slope, typically present as a cliff varying up to about 5-m high. (f) the *upper reef slope* is a subtidal area immediately to seaward of the outer lip.

On the north side of Heron Reef one more zone was sampled, the *inner lip* (Fig. 2). Between the reef crest and the reef slope an outer moat is present. This moat varies up to about 5-m deep and approximately 25-m wide. The lip of this moat as well as the outer lip was sampled on the north side. There is no outer moat on the south side in our sampling area.

Each subtransect of the seven transect series was  $2.5 \text{ m} \times 25 \text{ m}$ . In each of the seven transect series, two contiguous subtransects were made on the beachrock (giving a  $5\text{-m} \times 25\text{-m}$  sample area) and another two at the outer moat edge (because of low damselfish densities and their patchy distributions there). Three subtransects were run of the reef flat, one 50 m to seaward of the inner moat

Table 1. Sizes of six damselfish species

Species	Maximum Size of Collected Specimens*	
	Mass (g) <sup>†</sup>	Standard Length (mm)
<i>Po. flavicauda</i>	11	63
<i>Po. bankanensis</i>	13	64
<i>G. biocellatus</i>	19	76
<i>Po. wardi</i>	22	78
<i>P. lacrymatus</i>	30	80
<i>E. apicalis</i>	61	108

\* An attempt was made to collect the largest specimen of each species that we saw.

† Approximate size ranges of visually estimated size classes for each species: Juvenile  $\leq 1/4$  max. mass; Small  $> 1/4-1/2$  max. mass; Medium  $> 1/2-3/4$  max. mass; Large  $> 3/4$  max. mass.

series, one in the approximate center of the reef flat, and one about 50 m to shoreward of the reef crest. Two subtransects were run on the reef crest, one at the approximate center of the reef crest and one about 10 m inshore of the outer lip. The lip subtransects were run along the lip itself and those on the upper slope 5 m (horizontally) to seaward of the outer lip. In each of these subtransects, the numbers of individuals of each of the guild species were counted between mid- and full tide. Thus we were able to determine the relative abundances of each species in each zone.

### Associations of Individual Species with Specific Habitat Features

This consisted of making searches in attempts to determine if we could define a "habitat" for each of the six species, i.e., a substrate type with which it alone was associated. Such habitats could be on any scale—for example, living coral versus dead coral rubble, or large as opposed to small pieces of dead rubble. After an apparent association was detected, counts were made of the numbers of guild species associated with that habitat type over large areas of reef. In two cases in which there were extensive overlaps in the zonal distributions of pairs of species, we attempted to determine whether or not they showed microhabitat segregation in those areas; that is, whether there were different microhabitat features with which each species was associated.

Table 2. Relative abundances of six species of damselfishes in two series of transects on Heron Reef

Species	Transect Series*	Proportion Represented by Each Species of Fishes Counted in Each Subtransect							
		Beach Rock	Moat	Reef Flat	Inner Crest	Outer Crest	Inner Lip	Outer Lip	Slope
<i>Po. bankanensis</i>	South	—	—	—	—	—	†	.01	.02
	North	—	—	<.01	.04	.62	.58	.30	.28
<i>Po. flavicauda</i>	South	—	.12	.12	.17	.17	†	.04	—
	North	—	.11	.16	.88	—	—	—	—
<i>G. biocellatus</i>	South	.89	.02	<.01	—	—	†	—	—
	North	—	.11	—	—	—	—	—	—
<i>Po. wardi</i>	South	.11	.86	.88	.83	.83	†	.76	.74
	North	—	.78	.84	.08	.38	.33	.68	.56
<i>P. lacrymatus</i>	South	—	—	—	—	—	†	—	.10
	North	—	—	—	—	—	—	—	.01
<i>E. apicalis</i>	South	—	—	—	—	—	†	.19	.14
	North	—	—	—	—	—	.09	.02	.15
No. Fishes	South	35	463	723	195	170	†	152	91
	North	0	94	365	50	13	117	97	74

\* Data from 4 southside and 3 northside transects combined.

† No Inner Lip on south side—see materials and methods.

Table 3. Relative abundances of six damselfish species in coral-rich areas\* at the interface between intertidal and subtidal areas on two faces of Heron Reef

Species	Sites	Percentage of Sample Represented by Each Species				
		North Face†			South Face‡	
		Outer Crest	Upper Slope	Lower Slope	Outer Crest	Upper Slope
<i>Po. bankanensis</i>		54.8	49.3	56.8	13.2	87.7
<i>Po. flavicauda</i>		—	—	—	—	—
<i>G. biocellatus</i>		—	—	—	—	—
<i>Po. wardi</i>		43.5	49.2	30.9	85.6	12.3
<i>P. lacrymatus</i>		—	—	—	0.1	—
<i>E. apicalis</i>		1.7	1.5	12.4	1.1	—
Sample Size		473	533	259	907	269

\* Areas in which the substrate is >50% covered with shrubby growths of arborescent corals, mostly <15 cm high.

† North Face areas: Outer crest, within 5 m of outer edge of intertidal areas of reef (Sample area along 300 m of reef edge); Upper slope, ≈2.5 m deeper than crest (Sampled along 450 meters of reef edge); Lower slope, 2.5–4 m deep (sampled along 250 meters of reef edge). South Face areas equivalent to North Face areas (Both areas sampled along 600 m of reef edge).

## RESULTS AND DISCUSSION

### Patterns of Spatial Distribution of the Six Species

*Pomacentrus bankanensis*.—(a) Transects (Table 2): This species was originally thought to extend across the reef crest and outer half of the reef flat (Sale, 1978, Fig. 1). The few fishes on the south side transects were present only at the outer lip and subtidal slope. *Pomacentrus bankanensis* was much more abundant on the north side of Heron Reef, but again was concentrated at the seaward edge of the reef. On that side of Heron Reef, it was the most abundant guild member on the outer crest and inner lip. (b) Habitat association (Table 3): *Po. bankanensis* was often associated with solid coralline rock substrates containing a substantial cover of low, shrubby, branching corals (particularly of the genus *Acropora*) where such substrates occurred at the interface between intertidal and subtidal portions of the reef. On the north side of Heron Reef, this habitat type was more common than on the south side; it also extended into deeper water in the former area. *Pomacentrus bankanensis* was often the most abundant guild member in

Table 4. Relative abundances of six damselfish species on an intertidal rubble bank\* on the north side of Heron Reef

Species	Percent of Each Species Sample in Each Size Class†				Percent of Total Sample Represented by Each Species
	Juvenile	Small	Medium	Large	
<i>Po. flavicauda</i> n = 1255	3	17	44	36	98.0
<i>Po. bankanensis</i>	—	—	—	—	—
<i>G. biocellatus</i>	—	—	—	—	—
<i>Po. wardi</i> n = 24	88	8	4	0	1.9
<i>P. lacrymatus</i>	—	—	—	—	—
<i>E. apicalis</i> n = 1	100	0	0	0	<0.1

\* A rubble bank immediately inshore of a bare rock zone inshore of the reef crest. The sample covered 750 m of this bank which was up to 50 m wide. Substrate in which fishes were counted consisted of a coralline rock base covered with a moderate amount of small flat rubble chips 25–50 cm in diameter. All of this was covered with a fine film of sand and a distinct mat of fine algae up to approx. 0.5 cm thick. Fishes associated with large boulders were not included.

† See Table 1.

Table 5. Microhabitat segregation of *Pomacentrus flavicauda* and *Pomacentrus wardi* in two areas of intertidal reef flat

Microhabitat*	Number of Fishes of Each Species Counted in Each Microhabitat Type in Each of Two Areas			
	South Side of Cay		North Side of Cay	
	<i>Po. flavicauda</i>	<i>Po. wardi</i>	<i>Po. flavicauda</i>	<i>Po. wardi</i>
Low Rock and Rubble	136	296	206	159
High Rock	27	362	16	311

\* Low Rock and Rubble = Coralline rock boulders and coral  $\leq$  approx. 15 cm high, and  $<1$  m diameter. High Rock = Patches of coralline rock  $\geq$  30 cm high and  $>1$  m in diameter.

this habitat type, *Po. wardi* being the only other species commonly present. The greater abundance of this habitat type on the north side would explain why a species that was commonly associated with it was also more abundant in that area.

*Pomacentrus flavicauda*.—(a) Transects (Table 2): *Po. flavicauda* was originally thought to be restricted to the reef flat (Sale, 1978, fig. 1). Although it was common in that zone along our transects on the south side, it was also the second most abundant species on the reef crest and a few specimens were found at the outer lip. On the north side it was found in the same zones. Also, it was by far the most abundant species encountered on the north side along the transects of the inner reef crest. (b) Habitat associations (Tables 4 and 5): On the north side of Heron Reef, the very extensive reef crest contains banks of dead coral rubble with different types of rubble (in size, shape, etc.) being segregated in different zones. *Pomacentrus flavicauda* was virtually the only guild member present on one such type of rubble substrate (Table 4). *Pomacentrus wardi* was essentially the only other species present (it was commonest adjacent to large boulders, which were not included in these counts).

Table 6. Relative abundances of six damselfish species living adjacent to the intertidal beachrock\* on two sides of Heron Cay

Species	Side of Cay	Percent of Sample of Each Species in Each Size Class†				n	Percent of Total Sample Represented by Each Species
		Juvenile	Small	Medium	Large		
<i>Po. flavicauda</i>	South	—	—	—	—	0	—
	North	100	—	—	—	2	1.9
<i>Po. bankanensis</i>	South	—	—	—	—	0	—
	North	—	—	—	—	0	—
<i>G. biocellatus</i>	South	8	24	44	24	37	94.9
	North	23	13	35	29	79	76.0
<i>Po. wardi</i>	South	100	—	—	—	2	5.1
	North	65	30	5	—	23	22.1
<i>P. lacrymatus</i>	South	—	—	—	—	0	—
	North	—	—	—	—	0	—
<i>E. apicalis</i>	South	—	—	—	—	0	—
	North	—	—	—	—	0	—

\* Sampling areas included outer edge of beachrock, shallow moat to seaward of beachrock and areas immediately to seaward of that in which the only available solid substrate comprised small, scattered, isolated, low coralline rock slabs covering only about 10% of the bottom. These rock slabs were  $\leq 15$  cm high and  $\leq 1$  m diameter and were usually covered with a layer of silt. *G. biocellatus* adults excavated shelters under such rocks. The sampling area extended along about 400 m of shoreline on each side of the cay.

† See Table 1.

Table 7. Relative abundances of six species of damselfishes on coralline rock and coral masses at the west end of Heron Lagoon

Species	Percent of Each Species Sample in Each Size Class				Percent of Total Sample Represented by Each Species
	Juvenile	Small	Medium	Large	
<i>Po. flavicauda</i> n = 6	0	16	84	0	.06
<i>Po. bankanensis</i> n = 0	—	—	—	—	—
<i>G. biocellatus</i> n = 0	—	—	—	—	—
<i>Po. wardi</i> n = 1032	8	21	41	30	99.1
<i>P. lacrymatus</i> n = 3	—	100	—	—	.03
<i>E. apicalis</i> n = 0	—	—	—	—	—

*Pomacentrus flavicauda*'s spatial distribution overlapped most extensively with that of *Po. wardi*, which was more abundant throughout most of the areas shared by both (i.e., the reef flat). On both sides of Heron Island, we found evidence of microhabitat segregation of these two species on the reef flats. *Pomacentrus flavicauda* was relatively more common in areas of low, fragmented rubble than in higher, more extensive patches of coralline rock (Table 5). This pattern of *Po. flavicauda*'s association with low-profile rubble was also evident elsewhere. The rubble bank that was used almost exclusively by *Po. flavicauda* was composed of low, sand-dusted rubble chips, and the few *Po. flavicauda* present on the lagoonal patch reefs (where *Po. wardi* was abundant, see below) were living in areas of low rubble on sand.

*Glyphidodontops biocellatus*.—(a) Transects (Table 2): Sale (1978) indicated that this species was distributed across the inner half of the reef flat (his fig. 1) and that it was most common at the inner part of that zone and near the beachrock (Sale, 1974; Keenleyside, 1972). We found very few individuals on our reef flat transects. It was the most abundant species in the southside beachrock transects. It was also present in substantial numbers at the edge of the moat, although relatively not abundant. (b) Habitat association (Table 6): Individuals of *G. biocellatus*, and particularly the larger size classes of adults, were characteristically associated with low relief, sand-covered coralline rock. Adults often excavated burrows under such pieces of rock (Keenleyside, 1972). This was the most common guild member present in that type of habitat, with *Po. wardi* being virtually the only other species present. Also, while adults of *G. biocellatus* were well represented in that habitat, the *Po. wardi* present were mostly juveniles (Table 6).

*Pomacentrus wardi*.—(a) Transects (Table 2): Our data support Sale's finding that *Po. wardi* is the most widespread and abundant of the guild species—it was present in all the zones we sampled. It was also usually the commonest guild species in our samples. (b) Habitat association (Tables 7 and 8): As pointed out above, where *Po. wardi* co-occurred with *Po. flavicauda* these two species showed microhabitat segregation, with *Po. wardi* tending to be associated with

Table 8. Relative abundances of six species of damselfishes on 42 patch reefs\* in Heron Lagoon

Species	Percent of Each Species Sample in Each Size Class†				Percent of Total Sample Represented by Each Species
	Juvenile	Small	Medium	Large	
<i>Po. flavicauda</i> n = 62‡	3	15	21	61	2.7
<i>Po. bankanensis</i> n = 0	—	—	—	—	—
<i>G. biocellatus</i> n = 0	—	—	—	—	—
<i>Po. wardi</i> n = 2,262	12	19	41	28	97.2
<i>P. lacrymatus</i> n = 0	—	—	—	—	—
<i>E. apicalis</i> n = 0	—	—	—	—	—

\* Masses of coralline rock 5–25 m in diameter raised 1–2 meters above the sandy lagoon floor.

† See Table 1.

‡ All these *P. flavicauda* were in areas of low rubble and sand in the eroded crater-like centers of the patch reefs. *P. flavicauda* were present on 19 of the 42 patch reefs.

larger, higher pieces of coralline rock substrate. In areas well away from our transect sites, *Po. wardi* was also associated with this same substrate type; to the east of Heron Island, the reef flat type of substrate (coralline masses and rubble intermixed liberally with areas of sand) merges into larger areas of cavernulous coralline rock masses with relatively little sand or low rubble on sand. This formation continues towards the western end of the lagoon (Fig. 1). On these large expanses of coralline rock, *Po. wardi* was virtually the only guild member present (Table 7). In the Heron lagoon, one finds small patch reefs composed largely of coralline rock scattered about on a bare sand floor. *Pomacentrus wardi* was also virtually the only guild member found on these reefs (Table 8).

In the different types of habitats where *Po. wardi* was common, its population structure showed distinct differences. On the lagoonal patch reefs and at the western end of the lagoon, larger fishes predominated whereas on the reef flats and reef slopes around our transect sites the smaller size classes (especially juveniles) were relatively much more abundant (Tables 6 and 9).

*Plectroglyphidodon lacrymatus*.—(a) Transects (Table 2): Sale (1978) indicated that, on the south side, this species was found only on the subtidal portions of

Table 9. Population structures of *Pomacentrus wardi* at different sites on Heron Reef

Sites	n	Percent of Fishes in Each Size Class*			
		Juvenile	Small	Medium	Large
Lagoon patch reefs	2,262	12	19	41	28
Western edge of lagoon	1,032	8	21	41	30
South side reef flat	758	57	36	6	1
North side reef flat	468	61	30	9	0
South side reef crest and upper reef slope	807	51	44	4	1
North side reef crest and upper reef slope	542	41	51	8	0

\* For size classes see Table 1. Percentages based on visual estimates of size.

Table 10. Vertical zonations of *Plectroglyphidodon lacrymatus* and *Eupomacentrus apicalis*

Zones*	Number of Fishes of Each Species Counted in Each Zone			
	South Face		North Face	
	<i>P. lacrymatus</i>	<i>E. apicalis</i>	<i>P. lacrymatus</i>	<i>E. apicalis</i>
Upper Lip	1	224	0	39
Upper Slope	86	157	11	133
Lower Slope	457	61	72	256
TOTAL	544	442	83	428

\* Zones: Upper Lip, Interface between intertidal reef flat and subtidal reef slope; Upper Slope, From 1–2.5 m deeper than Upper Lip; Lower Slope, 2.5–7 m deeper than Upper Lip; South Face sampling area extended approx. 1 km along reef and North Face area along approx. 1.5 km.

the reef (see his fig. 1). In our transects, we also found it only on the lower reef slope where it was one of the less abundant guild species. (b) Habitat association (Tables 10 and 11): This pattern of *P. lacrymatus* tending to be most abundant in deeper subtidal areas showed up clearly in the counts we made of this species and *E. apicalis* at different depth profiles on the reef slope (Table 10). Also, *P. lacrymatus* was typically associated with “staghorn” type formations of *Acropora* spp. corals (Table 11). *Eupomacentrus apicalis* and *Po. wardi* were the only other guild species found in such dense staghorn beds, with the former being uncommon (Table 11) and the latter common. Sale also found that *Po. wardi* was more abundant than either *P. lacrymatus* or *E. apicalis* on the reef slope.

We found few juveniles of *P. lacrymatus* on the reef slope (or elsewhere) on either side of Heron Reef—they constituted 1.7% of 544 southside fishes and 4.8% of 83 northside fishes.

*Eupomacentrus apicalis*.—(a) Transects (Table 2): As Sale (1978, fig. 1) described, and our data also show, *E. apicalis* is an uncommon reef slope species. Although both *E. apicalis* and *P. lacrymatus* were previously thought to occur over the same types of habitats, our transect data suggest that *E. apicalis* is the more common one in the shallowest parts of the reef slope. (b) Habitat associations (Tables 10 and 11): The pattern of depth segregation of *E. apicalis* and *P. lacrymatus* showed up still more clearly in the counts that we made along three depth profiles on the reef slope (Table 10). These two species also showed microhabitat segregation in terms of the different types of substrate with which each was most commonly associated (Table 11), particularly on the south side of Heron Reef. Staghorn coral beds were quite rare on the north side, probably because of the greater damage that side suffers from storms and cyclones (Connell, 1976). On that side, *P. lacrymatus* was much less abundant than on the south side (Table 11) and microhabitat segregation between it and *E. apicalis* was less obvious than on the south side. This, we think, was probably a consequence of the lack of staghorn beds on the north side.

Our data show distinct substrate partitioning by *E. apicalis* and *P. lacrymatus* on the reef slope. Sale's transects in the same zone did not indicate such partitioning. We attribute this difference in results to differences in sampling methods and, probably, differences in the categorization of substrate types.

*Pomacentrus wardi* was common in all habitats used by *E. apicalis*, and we noted no apparent microhabitat segregation of the two species. *Pomacentrus wardi* and *P. lacrymatus* were the main guild species that co-occurred with *E. apicalis*. The remaining species to do so, *P. bankanensis* was most abundant in a habitat not well frequented by *E. apicalis* (Table 3).

Table 11. Microhabitat segregation of *E. apicalis* and *P. lacrymatus* at two sites

Microhabitat Type	No. of Fishes of Each Species Observed Living in Staghorn Coral ( <i>Acropora</i> spp.) Latticeworks as opposed to other Types of Substrates on Two Faces of Heron Reef			
	South Face‡		North Face‡	
	<i>E. apicalis</i>	<i>P. lacrymatus</i>	<i>E. apicalis</i>	<i>P. lacrymatus</i>
Staghorn lattices*				
Thin	63	8	—	3
Medium	39	156	—	—
Thick	34	368	—	—
Other substrates	204	1	78	63

	No. of Fishes of Each Species Living in Association with Ledges, and Otherwise, on Two Faces of Heron Reef			
	South Face‡		North Face‡	
	<i>E. apicalis</i>	<i>P. lacrymatus</i>	<i>E. apicalis</i>	<i>P. lacrymatus</i>
Fishes with ledges†	315	39	78	36
Fishes without ledges	105	607	0	27

\* Arborescent Lattices of *Acropora* spp. Thin = lattice works < approx. 12.5 cm thick. Medium = lattice works approx. 12.5–25 cm thick. Thick = lattice works > 25 cm thick.

† Ledges = coralline rock overhangs and corals growing in horizontal plates.

‡ Sampling areas were the same as those in Table 10.

In the subtidal portion of Heron Reef that we sampled, juveniles constituted only a small percentage of the *E. apicalis*—8.4 of 442 southside fishes, and 7.9% of 428 northside fishes. Thus juveniles of both *E. apicalis* and *P. lacrymatus* were much less abundant than those of *Po. wardi*, both relative to the numbers of adult conspecifics and to the numbers of contraspecific juveniles. Although our data were collected at only one point in time, larval recruitment of reef fishes in the immediate vicinity of Heron Reef is markedly seasonal (Russell et al., 1974), and our counts were made during the recruitment season.

Sale (1974) reported that *E. apicalis* shows a tendency to have aggregated territories. We found that both *E. apicalis* and *P. lacrymatus* tend to occur in colonies, i.e., aggregations in which several or more members of the same species often have contiguous feeding areas. On the south side of Heron Reef only 5.2% of the *E. apicalis* and 1.2% of the *P. lacrymatus* were not in mono- or bispecific colonies (as defined in Table 12). Colony formation was most noticeable in *P. lacrymatus*—72% of the fishes of that species were in colonies of 10 or more individuals, and the largest colony seen contained 47 individuals. Most colonies of these two species were monospecific, and the bulk of the population of each was in monospecific colonies. Mixed species colonies were the largest (Table 12).

#### Significance of Habitat Segregation and Specialization to the Coexistence of Guild Members

Our data have demonstrated that habitat segregation is more marked between the damselfishes than had previously been thought, although our transect data largely confirm Sale's transect data, and show extensive overlaps in the zonation patterns of various species. It has also been possible, in some cases, to demonstrate microhabitat segregation in areas of zonal overlaps.

These patterns of habitat segregation could be the result of either differences in species' resource requirements and habitat preferences in the absence of cur-

Table 12. "Colony" formation by *Eupomacentrus apicalis* and *Plectroglyphidodon lacrymatus* on the south side of Heron Reef

Type of Colony	Percent of Colonies That Are Each Type	Percent of Population of Each Fish in Each Colony Type	Number of Fishes in Each Colony Type ( $\bar{x} \pm 95\%$ C.I.)
<i>E. apicalis</i> only	47	72	4.7 $\pm$ 1.0
<i>P. lacrymatus</i> only	36	61	8.0 $\pm$ 2.5
Both species	17	—	6.0 $\pm$ 3.0
		<i>E. apicalis</i>	11.5 $\pm$ 4.9
		<i>P. lacrymatus</i>	

Sample sizes: 420 *E. apicalis* and 646 *P. lacrymatus* living in 136 colonies. A colony comprises two or more fishes whose feeding areas or algal mats come to within 1 m of each other.

rent competitive interactions, or differences in competitive abilities among species that are actively competing, or various combinations of these two effects.

It is evident, therefore, that substrate partitioning contributes significantly to the coexistence of various species of this group on both small and large scales. Such partitioning indicates that for each of the species there is a habitat type from which it cannot be competitively excluded by similar species, and explains how most of the entire pool of species can persist on a reef. The obvious cases in which space partitioning cannot, as yet, be invoked to explain species persistence are those of *E. apicalis* and *P. lacrymatus*. Individually, both of these species appear to overlap completely with and are involved in competitive interactions with *Po. wardi*. Sale's hypothesis is more relevant here than in other cases of species persistence.

Both Sale's data and ours show that *Po. wardi* is the most abundant and widely distributed of the six species. Sale has viewed *Po. wardi* as a fugitive species that is reliant for its continued existence on the space that is available in areas in which it is actively competing with other guild species. From our data, which show that *Po. wardi* occurs in abundance in large areas outside those it shares with other guild species, we argue that it should be considered the generalist of the guild, while the remaining five species, which do partition space on different scales, represent a group of five more specialized species.

The differences in the population structure of *Po. wardi* between habitats it shares with other species and those that it alone occupies support the notion that its adults are most successful in the latter habitat; and that this habitat type represents the preferred habitat of its adults.

#### Determinants of Dominance Relations in Fishes

In Sale's hypothesis, prior residence is considered to be of overriding importance in determining the outcome of intra- and interspecific competitive interactions with an individual of any species being able to retain a space it has occupied. However, two other factors besides prior residence often play a part in determining dominance relationships in fishes and other animals—(a) size differences and (b) species-specific differences in aggressiveness.

*Size Differences.*—The literature contains numerous examples of the advantage superior size can give in intraspecific aggressive interactions, and how it can override the effects of prior residence (Newman, 1956; Baird, 1968; Greenberg, 1947; Frey and Miller, 1972; Gorlick, 1976). Field and laboratory work on damselfishes has also indicated that such is the case in a variety of species of these

fishes, and that a size advantage can give priority of access to vacated space (Clark, 1970; Myrberg, 1972; Itzkowitz, 1977; 1978; Williams 1978). Sale's descriptions of relations between adult and juvenile damselfishes also indicate that juveniles are not totally capable of defending their territories against adults. Rather, they are able to remain in some areas because their small size allows them to shelter where adults cannot reach them. In several territorial Caribbean and Indian Ocean damselfishes, individuals of any size class are able to dominate much smaller conspecifics and enter the latter's territories with little or no resistance (D.R.R., unpublished data).

*Species-Specific Aggressiveness.*—Published evidence of interspecific differences in dominance ability among fishes is less evident (Kallenberg, 1958), although Williams (1978) has recently obtained data that point to one Caribbean territorial *Eupomacentrus* being able to aggressively exclude a congener from one habitat type. (However, it should be pointed out that the more dominant of these two species reaches twice the mass of the other in at least one site in which the two co-occur—D.R.R.)

*Interactions of Factors Determining Dominance Relations.*—Prior residence, size and species-specific aggressiveness have the potential to interact and affect dominance relations between individual fishes in a complex manner. For instance, prior residence can, up to a point, override a size advantage, as we noted above.

Work by one of us (D.R.R. et al., in prep.) shows that interactions between size and species-specific dominance ability influence dominance and spatial relations between individuals of different species of territorial damselfishes. Two species of Caribbean damselfishes in Panama frequently have (interspecifically) overlapping territories and feeding areas. One of these, *Microspathodon chrysurus*, grows to about six times the mass of the other, *Eupomacentrus dorsopunicans*. Individuals of *E. dorsopunicans* are able to exclude from their feeding areas individuals of *M. chrysurus* whose mass is less than, equal to, or up to about twice their own mass. When an *M. chrysurus* has a greater size advantage, it is able to dominate an *E. dorsopunicans* and superimpose its feeding area on that of the latter. *Microspathodon chrysurus* has a similar relationship with *E. planifrons*, which attains one-third the mass of *M. chrysurus*. However, large *M. chrysurus* are able to dominate and superimpose their territories on only those individuals of *E. planifrons* which are up to about half the latter's maximum size. Larger individuals can exclude any *M. chrysurus*.

Available data on interactions between *Po. wardi*, *P. lacrymatus* and *E. apicalis* do not permit a critical analysis of the relative importance of size, species-specific aggressiveness, and prior residence in determining dominance relationships.

#### Availability of Space for Different Guild Members and the Production of New Space

One of the central assumptions of the lottery hypothesis is that space used by all members of a set of competing species is saturated, and that the production of new space is beyond the control of those species. Physical factors are seen as the primary producers of new space.

We suggest that this may not be the case, that one or more of the guild members is capable of "creating" new space, and that there may be a surplus of the precursor that this species could alter to form new space. The explanatory potential of the lottery hypothesis is seriously diminished if we are correct in these suggestions.

Adults of at least one territorial Caribbean *Eupomacentrus* species, *E. planifrons*, regularly create their own habitat (patches of dead coral) by directly or indirectly killing living corals (Kaufman, 1977). One of us (D.R.R.) has been working on aspects of the ecology of this species, including such habitat formation, since Kaufman's discovery. Both *E. planifrons* and *P. lacrymatus* live in staghorn *Acropora* formations and defend and use distinct algal mats (Brawley and Adey, 1977) although *P. lacrymatus* mats are not as dense and conspicuous as those of *E. planifrons*. Some of the *P. lacrymatus* mats in staghorn beds at Heron Island contained large amounts of living coral. On some of those living coral branches there were lesions or blemishes that contained tufts of algae. Those lesions were similar in gross appearance to those that resulted from *E. planifrons* activity and which eventually led to the formation of algal mats maintained by that species. *Eupomacentrus apicalis* territories also contained coral with such "lesions" in a few instances.

Sale has suggested that areas of dead coral in which *Po. wardi* co-occurs, with *E. apicalis* and *P. lacrymatus* are produced by physical disturbances. However, in many areas used by *P. lacrymatus* (and, to a lesser degree, *E. apicalis*) this fish's territories were in coral growths that retained their original growth structure rather than being rubble. Therefore, it seems unlikely that physical disturbance had caused the death of many areas of coral that were used by *P. lacrymatus*.

The staghorn coral in which large colonies of *P. lacrymatus* were found often exhibited a characteristic structure. Coral branches in the center of the fish colony were nearly all dead while many of those around the edges were alive. Also, the coral in the center showed signs of having died well before that towards the edges, as the central material retained much less of its original structure. We suggest that this pattern of dead and live coral distribution could be the result of a (slow) process of formation, growth and/or movement of *P. lacrymatus* colonies. That is, the coral occupied first by the damselfishes had been dead longest and the most recently dead material, mixed with living coral, was that into which the fishes had most recently moved.

Further, it appeared that there could be a large surplus substrate that might be used as a habitat precursor by *P. lacrymatus*. On the south side of Heron Reef, its algal mats occupied only an extremely small proportion of the extensive staghorn beds in which it was most abundant. Experimental evidence is needed to determine whether the unused portions of the staghorn beds in that area represent suitable potential habitat for *P. lacrymatus*, and whether it is capable of modifying them for its use.

The tendency for *P. lacrymatus*, in particular, to form colonies is difficult to reconcile with the proposition that chance determines which species occupies space. Sale (1974) suggested that clumping of adult *E. apicalis* may be a social phenomenon. We are inclined to agree with this for both *E. apicalis* and *P. lacrymatus*, although some responses to habitat features are probably also involved. Some priority of access to space by these species at their colony sites is indicated.

#### Alternative Scenarios to Competitive Relations Between Species on the Local Scale

The data available are sufficiently inconclusive that they can be used to support more than one hypothesis. We suggest the following as an alternative to Sale's lottery hypothesis to explain how groups of species such as *Po. wardi*, *E. apicalis* and *P. lacrymatus* coexist on the small scale. In this alternative, we will assume that the space used by all three species is saturated, i.e., that *P. lacrymatus*

cannot create space. Although our hypothesis is less parsimonious than the lottery hypothesis, we have incorporated in it what we think are some of the complexities of the real world, as well as parts of the lottery hypothesis.

1. In some (many?) habitat subdivisions on a reef, interspecific competition for space is an ongoing process. Data: There are competitive interactions between *Po. wardi*, *E. apicalis* and *P. lacrymatus* on rubble patches, for example.

These habitat subdivisions may or may not represent the optimal or preferred habitat of (some age classes of) all the competing species. Data: Rubble patches may be suboptimal habitat for (adult) *Po. wardi*, which seems to do better in other areas.

Such areas supply the requirements of more than one species because (a) on a reef habitat features overlap and grade into one another rather than invariably being discrete and discontinuous, and (b) some species have more generalized habitat requirements than others. Data: *Po. wardi* is more generalized than either *E. apicalis* or *P. lacrymatus*.

2. Among the competing species there is an aggressive dominance hierarchy which is based on differences in species-specific aggressiveness, and/or differences in the maximum size each species attains. The more dominant species in such a hierarchy have priority of access to space. If differences in interspecific dominance ability are pronounced, the dominant species may be able to take control of any space, vacated or unvacated. If they are less pronounced, a dominant species may have priority of access only to a space that has become vacant. Data: *Po. wardi*, *P. lacrymatus* and *E. apicalis* reach quite different maximum sizes. Individuals of the smallest species, *Po. wardi*, are less able to retain control of space than are those of the other two species. Individuals of the largest species, *E. apicalis*, show a greater tendency to increase the amount of space they control by expanding their territories than do individuals of the other two species.

3. The aggressively more subordinate species persist in such overlap areas because the population densities of more dominant species (or the densities of those size classes of a dominant species that are able to dominate all size classes of a more subordinate species) do not reach the point at which they saturate the habitat they can use. This failure of a dominant species to reach saturation densities may be due to (a) mortality pressures independent of the competitive interaction (Paine, 1974; Connell, 1978). For example, larval or juvenile mortality might be higher in the more dominant species—both Sale's and our data indicate that larval settlement, or juvenile survivorship, is better in *Po. wardi* than in *E. apicalis* or *P. lacrymatus*—juveniles of *Po. wardi* were the most abundant of the three, both absolutely and relatively, in the general area where the three co-occurred. (b) Alternatively, it might be due to the interspecific dominance hierarchy being circumvented or overridden to some degree. The confounding effects of size differences and prior residence may, in combination with differences in the abundance of potential recruits of different species, put the smaller size classes of more dominant species at a disadvantage in competing for space. *Pomacentrus wardi* of all sizes are far more abundant than either *E. apicalis* or *P. lacrymatus*. Small individuals of these latter two species, both settling larvae and juveniles, may be at a disadvantage because *Po. wardi* that are sufficiently large to dominate them are superabundant and are able to take control immediately of most of the space that becomes available. *Pomacentrus wardi* provides the most recruits and *E. apicalis* the fewest of the three species. Differences in the timing of larval recruitment may also give *Po. wardi* an advantage in gaining control of space before larvae of more dominant species arrive.

### Coexistence on Large and Small Scales

It seems necessary, for several reasons, to consider competitive interactions between two or more species in one habitat type in the context of the types of interactions each of those species is involved in throughout its range on a reef. A "population" in one habitat type is not isolated from "populations" in other habitats because such fishes have highly dispersive larvae, and the persistence of a species in one habitat may be due in part to its success in another, noncontiguous habitat (Dale, 1978). *Pomacentrus wardi* is a case in point—its persistence in some of the many habitats in which it overlaps and competes with a variety of other species may be the result of its success in a habitat that covers large areas of reef away from the overlap habitats. It evidently has a large refuge, which may be important to its persistence as a species, and from which it disperses recruits to other habitats.

### CONCLUSIONS

Specialization plays a significant part in maintaining the coexistence of this group of species on both large and small scales, although it cannot be invoked in all cases.

Actively competing species sometimes have separate habitat refuges—other habitats in which they occur singly. However, other species may be actively involved in interspecific competition for space throughout their ranges. The lottery hypothesis has more relevance to the problem of small-scale coexistence of competing species than to the large-scale coexistence of those same species.

At least one of the guild species may be able to "create" suitable habitat. As there may be a surplus of the habitat that species could potentially use, space may not be saturated and all competitively interacting species may not be equally limited by its availability.

The existing data on relations between competing damselfishes support a hypothesis that differs in some respects from the lottery hypothesis, and that incorporates (a) several determinants of dominance relations among fishes (size differences, species-specific differences in aggressiveness, and prior residence), and (b) interspecific differences in mortality rates and recruitment rates.

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