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AVAILABILITY OF SPACE FOR THE TERRITORIAL CARIBBEAN DAMSELFISH *EUPOMACENTRUS PLANIFRONS*[1]

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Abstract. Populations of coral reef fishes are often thought to saturate habitable space and to be limited by its availability, particularly those fishes that defend space. In Panama, individual adults of the common Caribbean damselfish *Eupomacentrus planifrons* defend permanent, all-purpose territories. A territory contains a mass of coral from which the fish derives required substrate-based resources: shelter from predators, a nest site (males only), and food (from a distinct mat of algae). Two experiments tested whether an excess of suitable substrate was present in two of the main habitats of *E. planifrons*. (1) Coral substrate that contained algal mats was removed from small areas (up to 45 m^2) in habitats composed of *Agaricia* and *Acropora* corals. After 3 mo new algal mats were established on previously mat-free parts of the experimental areas, and the density of adult *E. planifrons* increased in the experimental areas. (2) The area of habitat of three small patch-reefs was reduced by one-half through the removal of coral substrate. One year later, the density of *E. planifrons* adults had increased on the remaining halves of those reefs. The results of both experiments indicated that a surplus of suitable substrate existed in the experimental areas and that *E. planifrons* was not generally limited by the availability of habitable space. Compared to control fish of the same length, experimental *E. planifrons* were similar in mass, in the amounts of fat reserves, and, in the case of females, in activity of their ovaries. Both experimental and control fish were breeding at the end of the experiment. Thus the experimental increase in population density did not appear to be detrimental to the physiological condition or reproductive capacity of the fish. We conclude that *E. planifrons* is probably not at the carrying capacity of the habitats it occupies.

Key words: Caribbean; carrying capacity; damselfish; Panama; Pomacentridae; population regulation; space; territoriality.

INTRODUCTION

Many reef fishes defend permanent general-purpose territories against both conspecifics and a range of other species of fishes, and both intra- and interspecific competition for resources are thought to be widespread among them (Low 1971, Brockman 1973, Barlow 1974*a*, *b*, Myrberg and Thresher 1974, Vine 1974, Reese 1975, Robertson et al. 1976, 1979, Ebersole 1977, Ehrlich et al. 1977, Nursall 1977, Sale 1977, Thresher 1977). The characteristic abundance of reef fishes that defend space has been an important factor promoting the belief that competition for space is prevalent and that suitable substrate is the major factor limiting reef fish populations (Smith and Tyler 1972, 1973*a*, *b*, 1975, Russell et al. 1974, Sale 1974, 1975, 1976*a*, *b*, 1977, 1978*a*, 1979 (but see Sale 1972), Ehrlich 1975, Smith 1975, 1977, 1978). Experimental documentation of this idea is generally lacking.

Here we describe an experimental test of the hypothesis that populations of the territorial reef fish, *Eupomacentrus planifrons*, are at the spatial carrying capacity of two habitats commonly occupied by it. If this hypothesis is correct, *E. planifrons* should be making full use of all suitable habitat, and any increase in its population density should be detrimental to the individual members of that population.

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THE BIOLOGY OF *EUPOMACENTRUS PLANIFRONS*

The three-spot damselfish, *Eupomacentrus planifrons*, occurs on coral reefs throughout the western Atlantic (Böhlke and Chaplin 1968, Randall 1968). It is one of the most abundant substrate-dwelling damselfishes on those reefs (Emery 1973, Clarke 1977, Itzkowitz 1977, Waldner and Robertson 1980, and see below). *Eupomacentrus planifrons* interacts directly with many species of plants and animals that commonly occur on Caribbean reefs. Individual fish defend territories against many other herbivorous, carnivorous, and omnivorous reef fishes (Itzkowitz 1974, 1977, 1978, Myrberg and Thresher 1974, Robertson et al. 1976, Thresher 1976*a*, *b*, 1977, Williams 1978), and omnivorous sea urchins (Williams 1979, 1980). The fish strongly influences the abundance and species composition of algae growing in its territories (Brawley and Adey 1977), and may have a major influence on coral community structure (Kaufman 1977).

The biology of this species makes it an ideal study subject. Males and females feed fairly exclusively on benthic algae and invertebrates (Randall 1967, Emery 1973, Lobel 1980). Males defend clutches of eggs that are attached to the substrate (Williams 1978). Adults typically defend a distinctive, discrete mat (a maximum of ≈70 cm in diameter) of thickly packed algae, which can grow to several centimetres in length (see Brawley and Adey 1977, Kaufman 1977). Adults frequently kill live coral as a means of establishing new substrate for the growth of an algal mat (Kaufman

1977). By this process a fish can expand an existing mat or move it slowly across the substrate, and can establish an entirely new one in an unused patch of completely live coral (Kaufman 1977, D. R. Robertson, *personal observation*).

METHODS

Study areas

All observations and experiments were made on patch reefs near San Blas Point, off the Caribbean coast of Panama. Reefs on the leeward side of the submarine extension of the Point were used. Data were collected between May 1977 and September 1979.

Eupomacentrus planifrons lives in many types of Caribbean reef habitats, but in our study area the species is characteristically associated with two common habitat types. One habitat is composed mainly of the hermatypic coral *Agaricia agaricites,* and to a lesser extent the hydrocoral *Millepora* spp., while the other main habitat consists of pure stands of the coral *Acropora cervicornis* (Waldner and Robertson 1980). We refer to these as the *Agaricia* and the *Acropora* habitats, respectively. The population structure of *E. planifrons* is quite different in the two study habitats: small fish predominate in *Agaricia* areas and large individuals in *Acropora* areas (Waldner and Robertson 1980). Thus large fish may be more likely to be limited by suitable substrate than are smaller fish because the *Acropora* habitat is less abundant than is the *Agaricia* habitat in San Blas (Waldner and Robertson 1980).

Abundance and spatial distribution

The abundance of *E. planifrons* relative to that of all other congeners present (*E. dorsopunicans, E. partitus,* and *E. leucostictus*) was estimated by counting fishes within a 1 m wide transect on a total of four patch reefs. Each of the transects, which ranged from 17–52 m in length, ran across the center of a shallow ($\leq$7 m depth) patch reef from its seaward side to its leeward side. These reefs were similar to the reefs used for experiments.

We mapped every adult *E. planifrons* feeding area that was partially or completely within the borders of the transect. The size of these feeding areas was determined by observing the foraging activities of each fish for a total of 10 min. Because the size of the area that an *E. planifrons* feeds in during 10 min is less than the size of its total feeding area, which in turn is smaller than the area it defends (see below), the amount of each transect occupied by total feeding areas and defended areas was estimated indirectly. For this estimation we independently determined the constants necessary to scale the size of defended areas relative to that of feeding areas. To determine the scaling constants, we chose 10 adult fish at random, and observed the activity of each during a 60-min time period. Three areas were mapped during this 60-min period: (1) the area that each fish fed in during the 1st 10 min of observation, (2) the total area each fish fed in during the entire 60-min period, and (3) the total area each fish defended (against all fish species) during the 60-min period. These data allowed us to estimate the size of each defended area on the transects from the size of each feeding area obtained by 10-min observations on the transects, and also standardized all our estimates of the size of feeding and defended areas on the transects to 60-min time periods.

We determined the pattern of spatial distribution of algal mats in both *Agaricia* and *Acropora* habitats by measuring the percentage of the circumference of each mat that was contiguous with other mats. Contiguous mats were defined as those <2.5 cm apart.

The rate of movement of algal mats was measured by mapping their borders, tagging them with aluminum discs, and then reexamining them after periods of up to 19 mo.

Resources derived from algal mats

We estimated the degree to which an algal mat and the substrate on which it grows provided the following resources.

Food.—We recorded where each of a series of adult *E. planifrons* took bites on the substrate during a single 20-min observation period.

Shelter from diurnal predators.—If a mat's substrate contains shelter used to avoid predators, then a fish should retreat to its mat area when attacked by a predator. The chance of observing an attack on a particular fish is extremely small. We therefore simulated attacks by shooting a small spear at a series of adult *E. planifrons*. The spear tip was covered with a cork, which reduced the possibility of seriously wounding the fish. We observed the reactions of one set of fish after being struck with the spear, and of another set to near misses by the spear. In both cases we noted where each fish hid (hiding was defined as a fish remaining relatively motionless in coral cover for at least 30 s).

Sleeping sites.—A three-spot damselfish usually sleeps within the area of its algal mat (Robertson and Sheldon 1979). A series of mats was checked 1.5 h after sunset for the presence or absence of sleeping fish. We assumed that a fish sleeping inside a mat area was that mat's owner.

Nest sites.—We determined the location of nests that contained eggs relative to the algal mat of a series of guardian males.

Experiments

We performed two similar experiments to test whether *E. planifrons* saturated its main habitats.

Algal mat removals.—The removal of all the substrate that contained the entire algal mats of individual *E. planifrons* was expected to lead to the establish-

ment of new mats on adjacent substrate and an increase in the density of *E. planifrons* on that adjacent substrate, if (1) an algal mat and the substrate supporting it supplied the resources its owner required, and (2) there was suitable unused substrate in the vicinity of existing mats.

Half-reef removals.—If suitable habitat on a reef was fully saturated, then the removal of all the habitat on half of the reef should not result in a change in the density of *E. planifrons* on the remaining half. An increase in density on the remaining half reef would indicate that excess suitable habitat was available. Further, if any resultant increase in the density of *E. planifrons* was not detrimental to individual fish, then their physical condition and reproductive activity should be the same as that of unmanipulated fish. This last expectation assumes that this species is reproductively active throughout the year. In San Blas, *E. planifrons* breeds during at least 11 mo of the year (September has not been sampled; G. Irvine, *personal communication* and D. R. Robertson et al., *personal observation*).

Successful establishment of new mats, an increase in population density, and the maintenance of reproductive activity would allow us to conclude that *E. planifrons* was not at the carrying capacity of the experimental habitats.

The two experiments were complementary. Although the algal-mat removals could have shown that vacant usable substrate existed, they would not show that additional fish could have established mats between those of the residents. If a fish defended an area that was larger than the area of its mats, then other fish could have been prevented from moving in. The half-reef removals were necessary to show that experimentally displaced adults could establish territories between those of the residents.

Experimental design

Algal-mat removals.—Experiment and control sites were situated in areas that contained both algal mats and mat-free live coral in both *Agaricia* and *Acropora* habitats. Algal mats covered 4–13% of the hard substrate in the *Agaricia* sites, and 5–28% of such substrate in the *Acropora* sites. In *Agaricia* habitat, six experimental sites on three reefs and six control sites on another three reefs were used. Experimental sites varied from 7.1–20.9 m^2 and each initially contained 16–23 algal mats. Control sites ranged from 5.5–16.4 m^2 and initially contained 15–28 algal mats per site. In *Acropora* habitat, seven experimental and seven control areas were used on a total of four reefs. Experimental sites ranged from 9.3–44.3 m^2 and initially contained 11–31 mats per site. Control sites covered from 7.4–23.6 m^2 and initially contained 11–21 mats per site.

At each site we mapped the locations of algal mats and of all adult and juvenile *E. planifrons* (juveniles were classified as fish <50 mm SL). In experimental areas, the coral substrate that supported individual algal mats was cut out completely and removed to sand areas 15–20 m away from the reef. Coral substrate at both the experimental and control sites rested on sand. The removal of each clump of mat-bearing coral replaced a usable piece of substrate with an unusable piece, because sand is rarely used as a mat substrate. In each experimental site in *Agaricia*, all the algal mats present were removed. Only 35–73% of the algal mats present were removed from each experimental site in *Acropora* habitat because more intensive removal would have seriously disrupted the physical structure of the areas of coral that remained.

Experimental sites were revisited 100 d after the manipulation. This time span was chosen to allow for the loss of fish that might have been forced into inadequate sites and (based on previous observations) to allow sufficient time for any new algal mats to form. We mapped the locations of all *E. planifrons* and the locations of any new algal mats. Similar mappings were made in control areas over the same 100-d period. To control for disturbance of the fish by the observer, we moved the coral bearing the algal mats slightly.

Changes in the density of fish and algal mats within experimental plots were determined by counting the total number of fish and mats in each plot, and by measuring the total area of coral substrate that remained in the plot after the removal of mat-bearing substrate. Changes in the density of fish and algal mats within each control plot were determined by counting the total number of fish and mats that occupied substrate which had been devoid of any algal mats at the start of the experiment, and by measuring the total area of this previously mat-free substrate.

Half-reef removals.—Reefs composed entirely of *Agaricia* habitat were used for this experiment because we could not find small isolated reefs composed of *Acropora* habitat. Three reefs were used: two were 5 m in diameter and the third 11 m in diameter. We mapped the positions of resident *E. planifrons* on one-half of each of the two small reefs, but only mapped the positions of resident fish in four 2 × 2 m quadrats on one-half of the largest reef. All coral and coral rubble protruding above sand on the unmapped half of each reef was then removed to sand 10–20 m away from the experimental reef. After 1 yr, we mapped the positions of fish on the undisturbed half of each reef.

Three reefs similar to the experimental reefs were used as control sites. On one of the control reefs, maps were made of the positions of *E. planifrons* resident in four 2 × 2 m quadrats, while a single quadrat of this size was used on each of the other two reefs. The locations of fish were mapped over the same 1-yr interval as that for the experimental reefs.

Samples of fish from experimental and control reefs

were speared at the end of the experiment. The following data were recorded for each fish: its standard length, the presence of fat deposits visible to the naked eye in the gut-mesentery, its sex, and the mass of the ovaries of females. These data were used to compare experimental and control fish in terms of their length/mass relationships, the size of their fat reserves, and the degree of reproductive activity of females.

RESULTS

The distribution and abundance of E. planifrons *and algal mats*

Eupomacentrus planifrons was the most abundant species of the genus within the transects and it accounted for over half of all fishes recorded. *E. planifrons* represented a mean of 59% (SE = 14.4) of the *Eupomacentrus* spp. individuals on the transects (n = 624) and *E. planifrons* adults represented a mean of 56% (SE = 13.4) of the *Eupomacentrus* spp. adults on the transects (n = 368).

From the sample of 10 fish, we calculated that the area a fish fed in during a 60-min observation was, on average, 1.5 (SE = 0.13) times the size of the area that it fed in during the first 10 min of observation. The size of each feeding area obtained from the four transects was scaled up to that of a 60-min observation period, using the mean (1.5) as the scaling constant. The area that a fish defended during the entire 60-min period was, on average, 3.7 (SE = 0.56) times the size of the area that it fed in during the initial 10-min period. This scaling factor was used to estimate the total defended area of each fish living on the four transects. Finally, the area a fish defended during the 60-min period was, on average, 2.5 (SE = 0.35) times the size of the area that it fed in during the 60-min period. Thus *E. planifrons,* as the most abundant fish found in the transects, only covered a mean of 36% (SE = 10.4) of the transect areas with its feeding areas, and its defended areas only covered a mean of 57% (SE = 14.1) of the transect areas.

Algal mats in *Acropora* habitat often touched one another, and in some areas were completely surrounded by as many as six other contiguous mats (Fig. 1). The majority of mats in *Agaricia* areas were not in contact with each other and very few mats were almost completely bordered by neighboring algal mats (Fig. 1).

Algal mats in both habitats moved slowly across the substrate. Sixteen mats in *Agaricia* habitat that were monitored over a 6.5-mo period moved at a rate of 0.6 ± 0.25 cm/mo (mean and 95% CI). Sixteen mats observed in *Acropora* habitat for 3.5–19 mo moved 1.4 ± 1.26 cm/mo. The mean diameter of mats (with 95% CI) in *Agaricia* habitat was 22 ± 0.7 cm (n = 324) and in *Acropora* habitat 45 ± 1.1 cm (n = 150). The magnitude of these rates indicates that an average algal mat may take from one to several years to move completely from its original position.

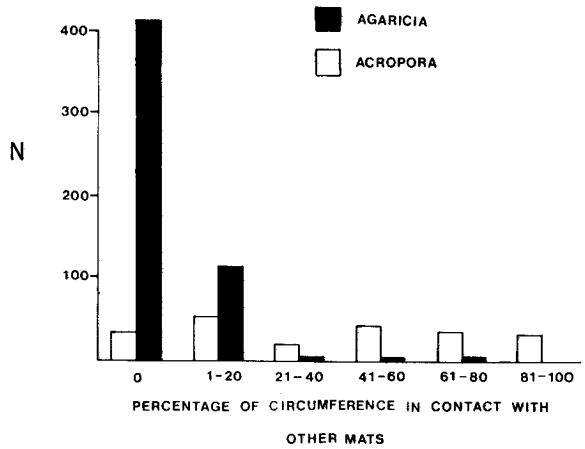

FIG. 1. Numbers of algal mats in *Agaricia* (n = 5 sites) and *Acropora* (n = 6 sites) habitats that have different percentages of their circumferences in contact with the edges of neighboring algal mats. Two mats are classed as in contact when they are ≤2.5 cm apart.

Use of the algal mat

The algal mat and its supporting coral appear to provide most or all of the substrate-derived resources that its owner uses. Almost all (mean = 95%, SE = 0.6%) of the substrate bites taken by 31 mat-owning *E. planifrons* were from their algal mats. Adults with mats also fed on nonsubstrate-derived food. The fish characteristically rose in the water column and fed intensively on concentrations of zooplankton that often moved across reefs in our study area. The great majority (89%) of the fish that received hits (n = 49) or near misses (n = 21) from a cork-tipped spear hid in the coral supporting their algal mats. Of 125 algal mats that were examined at night, 96% had adult *E. planifrons* resting in the coral supporting them. We found 78 *E. planifrons* nests containing eggs in *Agaricia* and 61 in *Acropora*; 96% of all nests were attached to the substrate inside the algal mat area.

Experiments

Algal mat removals.—The removal of algal mats in both *Agaricia* and *Acropora* habitats led to the establishment of new mats on adjacent coral substrate. In *Agaricia* but not *Acropora* habitat, some of the new mats partly covered the sides of excavations made by the initial removal of mats, but most (53 of a total of 63) were growing away from such excavations. In both habitats there were greater increases in the density of algal mats and of adult *E. planifrons* in experimental areas than were found in control areas, and the number of new mats in experimental areas was about half the number originally removed (Table 1). In contrast,

TABLE 1. Changes in the densities of algal mats and in the densities of adult *Eupomacentrus planifrons* 100 d after the removal of algal mats within study plots in two habitats. Values are mean (±SE). * $P < .05$, ** $P < .01$, Mann-Whitney U Test, probability that changes in experimental plots differ from changes in control plots.

		Habitat type	
		Agaricia	*Acropora*
Algal mats			
No. mats/m² prior to experimental removals	Experiments	1.86 (.249)	.82 (.147)
	Controls	1.88 (.482)	1.10 (.162)
No. mats/m² immediately after experimental removals	Experiments	0	.48 (.207)
	Controls	1.88 (.482)	1.10 (.162)
Increase in no. mats/m² at end of experiment	Experiments	.90 (.153) **	.38 (.094) *
	Controls	.08 (.040)	.07 (.052)
Fish			
No. adult fish/m² prior to mat removals	Experiments	2.89 (.510)	.94 (.128)
	Controls	2.54 (.445)	1.24 (.166)
Increase in no. adult fish/m² at end of experiment	Experiments	.95 (.333) *	.33 (.092) **
	Controls	.08 (.065)	.06 (.049)
No. of study plots	Experiments	6	7
	Controls	6	7

there were no significant differences between the changes in densities of juvenile *E. planifrons* in experimental and in control areas in either habitat (*Agaricia*: Mann-Whitney $U = 25$, $P > .20$, $n = 6, 6$; *Acropora*: $U = 21$, $P > .20$, $n = 7, 7$).

Half-reef removals.—The density of adult *E. planifrons* increased on the coral area that remained following the removal of half of each of the experimental reefs (Table 2). Population density increased to between 1.25 and 1.63 times the original densities on experimental reefs and these increases were consistently greater than those in control areas. The densities of juvenile *E. planifrons* generally decreased in both experimental and control areas, and the decreases were greatest in the control areas (Table 2).

Fish collected on the experimental reefs at the end of this experiment had body masses similar to those of control fish of the same length (test for coincidental regressions, Zar 1973:234; $F = 1.9$, $P > .50$; $n = 36$ experimental fish, 64 control fish). The increased den-

TABLE 2. Changes in the density of *Eupomacentrus planifrons* on undisturbed halves of patch reefs 1 yr after the removal of the other half of each experimental reef.

		Initial densities (no. fish/m²)			Changes in densities (no. fish/m²)	
		Experimental reefs		Control reefs	Experimental reefs	Control reefs
	Reef no.		Reef no.			
Adult *E. planifrons*	1	2.00	4	2.00	+1.25	−1.00
	1	2.00	4	2.00	+0.75	−0.25
	1	1.50	4	2.25	+0.50	−0.75
	1	2.00	4	1.50	+1.25	0
	2	1.94	5	1.33	+1.11	+0.44
	3	0.97	6	0.50	+0.24	+0.50
					Mann-Whitney $U = 34.5$, $P < .01$	
	Reef no.		Reef no.			
Juvenile *E. planifrons*	1	1.25	4	4.00	−0.75	−2.75
	1	1.00	4	3.25	−0.25	−2.25
	1	1.00	4	4.50	−0.75	−3.25
	1	0.50	4	3.25	−0.50	−2.75
	2	0.83	5	2.00	+1.11	−0.67
	3	3.41	6	5.75	0	−3.00
					Mann-Whitney $U = 53$, $P < .01$	

TABLE 3. Comparisons of the levels of ovarian activity and the sizes of fat deposits in two classes of *Eupomacentrus planifrons*: experimental animals, whose population density was increased, and control animals.

A. The number of females >50 mm SL that had either active or inactive ovaries.*

	Experimental	Control	
Active ovaries	10	10	$\chi^2 = 2.8$, $P > .10$
Inactive ovaries	6	14	

B. Number of fish >50 mm SL that had fat deposits in their gut mesenteries.†

		Experimental	Control	
Males	With fat	4	11	$\chi^2 = 0.75$, $P > .50$
	Without fat	5	24	
Females	With fat	1	3	$\chi^2 = 0.57$, $P > .50$
	Without fat	15	21	

* Active = ovary mass ≥1.5% of body mass, contains well developed to ripe eggs. Inactive = ovary mass <1.5% body mass, individual oocytes not apparent to naked eye.

† With fat = fat in the mesentery as strips (up to ⅓ the diameter of the intestine) which were readily visible to the naked eye. Without fat = no deposits visible to the naked eye.

sity of fish on experimental reefs did not lead to significant differences between the proportions of experimental and control females that had active ovaries (Table 3A), and did not lead to significant differences between the amount of mesenteric fat deposits of experimental and control fish (Table 3B). Further, we observed males guarding clutches of eggs on both experimental and control reefs when the experiments were terminated.

DISCUSSION

The area of coral substrate that contains the algal mat of an adult *E. planifrons* appears to supply almost all of the substrate-derived resources that its owner is currently using and defending. This "resource area" is the only exclusive portion of a fish's territory and it comprises only about 40% of the total area defended (i.e., the defended area is about 2.5 times the size of the feeding area). The resource areas of neighbors do not overlap, but the defended areas of neighbors may overlap considerably when the fish are close together. The complex nature of territoriality in *E. planifrons* has been demonstrated by Myrberg and Thresher (1974), who found that a fish maintains a series of territories (defended areas) that differ in size according to the species of fish that the territory owner is responding to.

The nature of area defense by *E. planifrons* is even more complex than those authors suggested because the area(s) that a fish defends is not necessarily equivalent to the area that contains its defended resources. We suggest that the defended area of an *E. planifrons* is much larger than its resource area for the following reasons. An algal mat covers a relatively small area and it contains a large concentration of food. Many species of reef fishes would feed on this resource and rapidly deplete it if it was left undefended (see Robertson et al. 1976, Lobel 1980). It is advantageous for an *E. planifrons* to be highly aggressive because it is defending concentrated, vulnerable resources, and probably the efficacy of its defense is increased when potential intruders are attacked well before they reach those resources. It is easy for an *E. planifrons* to move rapidly outside its mat area because the diameter of an algal mat typically is less than five times the length of the fish that owns it. This means the cost of defending the extra area outside the resource area is low relative to the benefits accrued by such defense. Robertson et al. (1979) have described a similar situation among some Indian Ocean surgeonfishes that defend highly concentrated food resources against a large range of fishes.

It is conceivable that the mat-free substrate around existing mats might represent either a "buffer" zone that each individual requires around its algal mat, or substrate onto which the fish will move or expand its mat in the near future. However, our data do not indicate that such is the case. First, in some areas of *Acropora* habitat, mats are often partly or completely surrounded by contiguous mats, and thus they lack a complete "buffer" zone. Second, mat-free substrate adjacent to a mat often remains unused for a considerable time; mats are often stationary, and when they do move, they move slowly.

The algal mat removal experiments indicate that adult fish that are dispossessed from their mats can set up new algal areas on adjacent substrate, even under conditions of increased population density. Thus a surplus of suitable substrate appears to exist in the experimental habitats, and our results indicate that some areas could support about 50% more mats than they presently do.

The half-reef removal experiments demonstrate that short-distance movements by adult *E. planifrons* can result in increased densities of fish to levels about 50% greater than premanipulation levels. These density increases do not appear to be detrimental to an individual's ability to survive and reproduce because fish do

not lose either mass or fat reserves, females maintain gonadal activity at the level found in control sites, and fish continue to breed. While these results do not show conclusively that the fitness of experimental and control fish was the same at the end of the experiment, they do support such an idea. The ability of fish to move and thereby increase densities leads us to suggest that fish could also have moved into the areas from which we removed individual algal mats and set up additional mats among those of resident territory owners. We think that *E. planifrons* can move and set up new resource areas between those of resident conspecifics because a fish requires and enforces exclusive use of only part of its defended area. We expect that adults that move generally establish themselves outside the exclusive-use portions of the residents' defended areas.

The increases in the densities of adult *E. planifrons* that resulted from experimental manipulations were not accompanied by decreases in the densities of juvenile conspecifics greater than decreases in the control areas. This result indicates that (unlike the situation observed by at least one other worker; Sale 1976*b*) juvenile densities of *E. planifrons* are not necessarily regulated by juvenile-adult interactions.

We conclude that adults of *E. planifrons* are not at the spatial carrying capacity of two of the species' main habitats in San Blas. Adult densities could be increased without apparent detriment to the existing populations of adults and without reducing the recruitment of young fish. If space is not generally limiting populations of *E. planifrons* on reefs in our study area, then what is? Food availability may limit an individual's growth and reproductive rates; an adult's use of food that is not derived from algal mats suggests that a mat may not provide food of sufficient quality or quantity for maximizing growth and reproductive rates. It may be that levels of juvenile recruitment are insufficient to maintain populations at saturation levels, and/or predation may be keeping numbers of one or more size classes below saturation levels. These latter mechanisms have yet to be tested under controlled field conditions.

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