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INTERSPECIFIC COMPETITION CONTROLS ABUNDANCE AND HABITAT USE OF TERRITORIAL CARIBBEAN DAMSELFISHES[1]

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Abstract. The prevailing notion that interspecific competition has little impact on the abundances of tropical reef fishes has been tested by few experiments, all of which examined its effects on recruitment and juvenile demography rather than on adult abundances. This study, in Caribbean Panama, examined whether a common territorial damselfish, *Stegastes planifrons,* limits the abundances of adults of four ecologically similar congeners in *S. planifrons*' primary habitat: *S. partitus* and *S. variabilis,* which commonly occur in that habitat, and *S. diencaeus* and *S. leucostictus,* which rarely do.

When *S. planifrons* was nearly eliminated from 16 natural patch reefs for 4–6 yr, adult populations of *S. partitus,* which is less aggressive and half the size of *S. planifrons,* doubled and expanded their range into a microhabitat previously used almost exclusively by adults of *S. planifrons.* Population increases by *S. partitus* occurred within 1 yr of the removal of *S. planifrons,* were persistent, but only reached their maximum ≈4 yr (and about four generations) after the initial removal. Adult populations of *S. variabilis,* which is less aggressive and 20% smaller than *S. planifrons,* also doubled following the removal of *S. planifrons.* Combined populations of *S. partitus* plus *S. variabilis* increased most on reefs where *S. planifrons* previously had been most dense. However, increases by those two species reached only ≈70% of the population density and ≈40% of the biomass density that *S. planifrons* had before the removals. Removal of *S. planifrons* had no effect on the abundances of *S. diencaeus* and *S. leucostictus.* Removal of *S. partitus* from eight reefs for 3 yr did not affect the abundances of *S. planifrons* or *S. variabilis.*

Eleven years monitoring of adult populations and juvenile recruitment by *S. partitus* before and during the experiment show that its population increase after the removal of *S. planifrons* occurred while its overall abundance was gradually increasing, but was not associated with a period of unusually high juvenile recruitment.

Thus asymmetric competition among closely related, ecologically similar, territorial coral reef fishes does sometimes control both abundances and microhabitat use in shared habitat. Interspecific territoriality and differences in body size and aggressiveness that lead to asymmetric competitive ability occur commonly among reef fishes in various trophic groups. Interspecific interactions within such groups of species often affect their patterns of habitat use. Hence the role that interspecific competition plays in limiting abundances of coral reef fishes requires reevaluation.

Key words: Caribbean; coral reef fish; damselfish; interspecific competition; population limitation; recruitment; territoriality.

INTRODUCTION

A central question in marine ecology arises from the fact that marine organisms often begin life as pelagic larvae: to what extent are marine benthic communities organized by interactions among benthic populations vs. the dynamics of the influx of pelagic recruits (e.g., Lewin 1986, Roughgarden et al. 1988, Underwood and Fairweather 1989)? Ecologists who first became interested in factors that determine the abundances of coral reef fishes were seeking to explain how the great numbers of species of fishes found on reefs coexist. They assumed that competition within such communities is a major organizing factor (Smith and Tyler 1972, Roughgarden 1974, Ehrlich 1975, Sale 1977, Gladfelter et al. 1980, Robertson and Lassig 1980, Anderson et al. 1981). Subsequently, the realization that fluctuations in the recruitment of those fishes often strongly influence their population dynamics led to the view that recruitment variation is of primary importance in controlling their abundances and spatial distributions (Doherty 1981, 1983, Victor 1986, Doherty and Williams 1988*a*, *b*, Wellington and Victor 1988, Doherty and Fowler 1994*a*, *b*). More recent work has shown that effects of recruitment patterns can be modified by benthic processes that affect the growth and survival of juveniles, and the spatial distributions of adults (Jones 1987*b*, 1990, 1991, Shulman and Ogden 1987, Robertson 1988*a*, *b*, Forrester 1990). However no experimental studies have tried to assess the relative influences of recruitment and a broad range of postrecruitment processes on the distribution and abundance of any tropical reef fish through adulthood.

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The current perception of the importance of competition in tropical reef fish communities has recently been summarized as follows: (1) Intraspecific competition can have substantial effects on population structure and adult abundance through its effects on juvenile growth and survival. (2) Known effects of interspecific competition include only limitation of local habitat use, and there is virtually no evidence that such competition affects population size (Ebeling and Hixon 1991, Jones 1991, Sale 1991, Williams 1991). However, experiments on the influence of interspecific competition on the abundances of tropical reef fishes have focused on its effects on larval recruitment and/or the survival and growth of juveniles (Doherty 1982, 1983, Shulman et al. 1983, Sweatman 1985, Jones 1987*a*, 1988). No experimental studies on those fishes have examined the most important demographic consequence of interspecific competition, its influence on adult abundance, or tested for a linkage between its effects on abundance and habitat use. In contrast, experiments have shown that interspecific competition does limit both habitat use and abundance of adults of temperate reef fishes (Hixon 1980, Larson 1980, Holbrook and Schmitt 1989, Schmitt and Holbrook 1990).

The present study was intended to address the absence of experimental assessments of the effect of interspecific competition among tropical reef fishes on adult abundance. In selecting the species, habitat, and type of experimental manipulations I thought it would be most useful to begin by determining what effects such competition has where and how it seemed to have reasonable potential to be operating. Interspecific competition occurs most frequently among species that have high overlaps in diet and microhabitat use (Schoener 1983), although static patterns of overlap in resource use alone are not good predictors of its occurrence (Holbrook and Schmitt 1989, Schmitt and Holbrook 1990). Interspecific competition usually has asymmetric effects (Connell 1983, Schoener 1983), with larger species being competitively superior (Schoener 1983, Brown and Maurer 1986), at least when interference competition is involved (Persson 1985). I worked with a congeneric group of common reef fishes whose adults have similar diets, individually defend exclusive-use, general purpose territories against each other, differ in body size and aggressiveness, and share habitat to varying degrees. I examined relations between five of those species in one habitat in which their abundances differed greatly, aiming to answer the following questions about interactions among them: (1) Do populations of one species in its primary habitat limit the abundance of two congeners that commonly occur in that habitat, and two congeners that rarely use that habitat? (2) Are any limiting effects of competition on abundance coupled to limitation of microhabitat use? (3) Are any effects of competition asymmetric, with larger, more aggressive species being less affected? (4) What is the magnitude of any effect of competition on the densities of affected species, relative to their normal densities and those of their competitors? (5) How quickly does any release from competition lead to an increase in abundance and how soon does any such compensatory response reach its maximum extent? (6) Is any interspecific limitation of the abundance of a species the normal state for it, or an infrequent occurrence arising from unusually high juvenile recruitment by it?

Materials and Methods

Study area

Field work was conducted at Punta de San Blas (9°34′ N, 78°57′ W) on the eastern Caribbean coast of Panama (map in Robertson 1987).

Study species and their biology

There are six species of the damselfish (Pomacentridae) genus *Stegastes* on Caribbean coral reefs: *S. diencaeus, S. dorsopunicans, S. leucostictus, S. partitus, S. planifrons,* and *S. variabilis.* Adults of *S. diencaeus, S. dorsopunicans,* and *S. planifrons* are strongly aggressive and defend exclusive-use, single-owner, general-purpose territories against conspecifics, congeners, and many other benthic feeding fishes (Robertson et al. 1976, 1981, Itzkowitz 1977, Robertson 1984). Adults of *S. leucostictus, S. partitus,* and *S. variabilis* also defend such territories (Itzkowitz 1977, Gronell 1980, D. R. Robertson, *personal observations*), but are less aggressive than the former three. Territories of *S. variabilis* often contain those of *S. partitus* (Waldner and Robertson 1980). Adults of *S. diencaeus, S. dorsopunicans,* and *S. planifrons* are more strongly reliant on benthic algae for food than *S. partitus,* which commonly feeds on both planktonic and benthic material, or *S. leucostictus* and *S. variabilis,* which are more omnivorous benthic feeders (Emery 1973, Robertson 1984). *Stegastes planifrons* is an abundant, ecologically important species that strongly influences many organisms on Caribbean reefs (Kaufman 1977, Williams 1980, Knowlton et al. 1990).

With a median mass of 11 g, adults of *Stegastes planifrons* are about twice as heavy as those of *S. partitus* and *S. leucostictus* (median = 5 g in both cases), ≈20% heavier than those of *S. variabilis* and *S. dorsopunicans* (median = 9 g in both cases), but half the mass of those of *S. diencaeus* (median = 22 g) (Robertson 1995). Prior to the manipulations adults predominated in the populations of *S. planifrons* (61%), *S. partitus* (67%), and *S. variabilis* (63%) on the experimental reefs.

All six species produce pelagic larvae, which spend ≈1 mo in the oceanic environment before settling into reef habitats (Robertson et al. 1993). Hence their populations presumably are open, with juveniles recruiting to reefs other than those on which they were spawned.

Habitat use by Stegastes *species*

The six species of *Stegastes* vary in the extent to which they share habitats on reefs in San Blas (Waldner and Robertson 1980, Robertson 1984, 1995, and elsewhere in the West Atlantic (Emery 1973, Clarke 1977, Itzkowitz 1977, Wellington 1992). In San Blas, four species have refuge habitats, in which each is virtually the only species found and adults are a major component of its population: *S. planifrons* in areas of continuous hard substrata, primarily composed of *Agaricia* corals, at ≈1.5–10 m depth on the sides of reefs; *S. partitus* in areas of sponges growing on sand; *S. variabilis* in deep (>10 m) noncontinuous coral habitat; and *S. dorsopunicans* on the semi-emergent tops of reefs. *S. leucostictus* and *S. diencaeus* are largely restricted to shallow (<2 m depth) backreefs, where other congeners also are abundant.

The experiments discussed here were performed on small submerged patch reefs composed of the same coral substrata as found at 1.5–10 m depth on the reef slopes of large emergent reefs. To define the extent of use of this habitat by the *Stegastes* species I censused them on three types of reefs: (1) one large emergent reef on which coral growth extended down to 30 m depth (censused in 1987), (2) three emergent patch reefs growing in shallow (7 m depth) seagrass (censused in 1993), and (3) the 40 experimental patch reefs, which were low relief (0.5–1.5 m high) reefs at 2–8 m depth (censused in 1987). During those censuses I counted the total number of individuals of each species present in (a) three 5 m wide, 105–175 m long, belt transects running from shallow to deep habitat across the large emergent reef, (b) the entire reef slope of each of the three small emergent patch reefs, and (c) each entire experimental reef.

Experimental manipulations

If the habitat use and abundance of one species is limited by competition with another then the removal of the latter should result in the former expanding into the latter's habitat and becoming more abundant. The removal experiments described here were intended to test mainly for effects of *S. planifrons* on *S. partitus* and *S. variabilis,* and reciprocal effects of *S. partitus* on *S. planifrons.* I concentrated on interactions between *S. planifrons* and *S. partitus* because they are the most abundant species in the habitat in which the experiments were performed (see *Results*). There were three treatments: (a) *S. planifrons* removal—all *S. planifrons* were removed from a patch reef and the changes in density of *S. partitus* and *S. variabilis* were measured; (b) *S. partitus* removal—all *S. partitus* were removed from a patch reef and the changes in density of *S. planifrons* and *S. variabilis* were measured; and (c) Control—changes in densities of all three species on an undisturbed patch reef were measured concurrently with those on a removal reef. I used isolated patch reefs for these experiments to facilitate the maintenance of the treatments. When damselfishes are cleared from small areas on large reefs conspecifics rapidly move into those areas from surrounding habitat (e.g., Waldner and Robertson 1980). Such behavior can be a general problem for maintaining removal treatments in small sections of large areas of habitat (McNally 1983).

Prior to the removals juveniles and adults of each species were censused on each reef. A minimum-sized adult embedded in a block of clear plastic was used as an aid in distinguishing adults during those censuses (all species of *Stegastes* readily approach and closely inspect such models of conspecifics placed in their territories). During the preremoval censuses for the *S. planifrons* removal experiment the location of the territory of each adult of *S. partitus* and *S. planifrons* on each reef also was recorded. Those adults were classed as being in either "edge" or "central" locations, i.e., less than or more than ≈30 cm from an interface between raised coral substratum and sand. Immediately after the initial censuses the appropriate removals were made using microspears and quinaldine anaesthetic administered by a squeeze-bottle to individual fish. Initial removals were 95–100% effective. The treatments were maintained by making further removals at 4–6 mo intervals thereafter. Densities of juveniles and adults of the removed species did not rise above ≈15 and 10%, respectively, of their premanipulation levels between those periodic removals. At yearly intervals after the initial removals I recensused the damselfish populations on all reefs. During the final census of the *S. planifrons* removal experiment I again determined the positions (edge or center) of adults of *S. partitus* on each removal and control reef.

Due to difficulty in finding suitable patch reefs at a range of locations I started eight replicates (each consisting of one removal reef plus one control reef, see *Data analyses* below) of the *S. planifrons* removal experiment in 1987, added three more replicates in 1988, and five more in 1989. This experiment ran through 1993, i.e., for 4–6 yr in the different replicates. All eight replicates of the *S. partitus* removal experiment were started in 1987. This experiment was terminated 3 yr later, when the abundance responses of *S. planifrons* and *S. variabilis* were clearly defined. One set of 16 patch reefs acted as controls for both the *S. planifrons* removal experiment (n = 16) and the *S. partitus* removal experiment (n = 8), with eight reefs acting as a control in both experiments.

This study was performed in natural patches of habitat and incorporated natural spatial variation in conditions. Previous experimental studies of competition among tropical reef fishes attempted to minimize effects of variation in factors such as reef location, size, isolation, habitat structure and fish density. They did so by manipulating and standardizing habitat patches and fish densities (Doherty 1982, 1983, Shulman et al. 1983, Sweatman 1985, Jones 1987*b,* 1988). Here I sim-

TABLE 1. Characteristics of experimental patch reefs and their associated populations of *Stegastes* spp.

	Treatment		
	S. planifrons removal	Control	*S. partitus* removal
Patch reef characteristics			
Median (range) area of reef (m^2)	71 (4–121)	50 (4–133)	44 (11–77)
Relative sizes of paired reefs			
Removal larger	$n = 7$		$n = 6$
Control larger	$n = 9$		$n = 2$
Median (range) distance to paired control reef (m)	30 (10–600)	NA	25 (15–100)
Median (range) distance to nearest other reef(m)	20 (5–25)	15 (5–20)	15 (5–20)
Adult damselfish densities prior to removals			
S. planifrons: median (range) no. adults per m^2	0.59 (0.14–1.41)	0.62 (0.10–1.50)	0.85 (0.20–1.23)
Removal > control	$n = 8$		$n = 5$
Control > removal	$n = 8$		$n = 3$
S. partitus: median (range) no. adults per m^2	0.20 (0–0.53)	0.23 (0.04–0.83)	0.32 (0.18–0.96)
Removal > control	$n = 8$		$n = 5$
Control > removal	$n = 8$		$n = 3$
S. variabilis: median (range) no. adults per m^2	0.10 (0–0.21)	0.10 (0–0.24)	0.06 (0–0.11)
Removal > control	$n = 4$		$n = 3$
Control > removal	$n = 6$		$n = 3$
Removal = control	$n = 2$		$n = 2$

ply used whatever patch reefs of a suitable size (i.e., small enough to be able to manipulate fish populations) I could find in a range of locations.

The experimental patch reefs were scattered haphazardly about in an area ≈2 km^2. Habitat on them consisted of varying proportions of coralline rock, dead and live corals (mainly *Agaricia* species, plus smaller amounts of *Montastraea, Siderastrea,* and *Diploria*), sponges, macroalgae, and large gorgonians. There also was considerable variation among both removal and control reefs in size, degree of isolation, proximity to oceanic inflow into the reef system, and the population densities of different *Stegastes* species (Table 1). However, there were no consistent patterns of difference between the removal and control reef of each replicate (Table 1) that would seem likely to have biased the results. In five replicates both the removal and control reefs were quite close (≈5 m) to other reefs. In the other replicates the reefs were at least 20 m from another reef. Measurement of the effects of a host of factors other than the populations of *S. planifrons* or *S. partitus* would have required a much larger sample of reefs than was logistically feasible.

On reefs from which *S. planifrons* were removed I also removed *S. dorsopunicans.* The rationale for this was that the removal of *S. planifrons* was intended to test for effects of a highly aggressive species on less aggressive ones, and *S. dorsopunicans* and *S. planifrons* are ecologically similar and both strongly territorial. *S. dorsopunicans* was present on 31% of the removal reefs and 38% of the control reefs, but constituted <6% of the combined population of all *Stegastes* species on them. For brevity, reference to removals of *S. planifrons* also covers those of any *S. dorsopunicans* and this experiment is referred to as the *S. planifrons* removal experiment.

Data analyses.—To assess the effects of competition and minimize those due to spatial variation in other factors, I compared the responses of fish on pairs of removal and control reefs that were composed of similar habitat and were situated in the same general part of the study area. I used Wilcoxon paired-sample tests to compare the change in population density of the "affected" species over a particular period (year 0 to year 1, . . . year 0 to year 6) on each removal reef and its control reef. I used one-tailed tests because the competition hypothesis predicts a directional population response. Significance levels were corrected for multiple comparisons using the Sequential Bonferroni Technique (Hochberg 1985). Changes in both adult and total populations were compared. The latter included all fish except recruits-of-the-month. Pelagic recruits of reef fishes often arrive patchily and in abundance (e.g., Doherty 1991) and experience high early mortality (Sale and Ferrell 1988, Booth 1991). They were not included in these analyses because they could numerically dominate a local population temporarily, while representing a trivial proportion of its biomass.

I also used Wilcoxon paired-sample tests to compare (a) natural patterns of microhabitat use by adults of *S. partitus* and *S. planifrons* prior to the removal of *S. planifrons* (by comparing the percent of adults of each species in central positions on the same reef), and (b) change in microhabitat use by adults of *S. partitus* on the removal and control reefs following the removal of *S. planifrons* (by comparing the percent of adults in central positions before the removals and at the end of the experiment on the same reef).

Adults of *Stegastes partitus* sometimes occur at high local densities. All reefs used in the *S. planifrons* removal experiment were of sufficient size to support numerous *S. partitus* and all were used in the analyses

TABLE 2. Use of the primary habitat (the reef slope at 1.5–10 m depth) of *Stegastes planifrons* by populations of two other congeners.

Reef	Area (ha)	Percent* of population† of each species‡ on reef slope						Percent* of combined population† of three species‡ on reef slope			
		S. plan.	*n*	*S. part.*	*n*	*S. var.*	*n*	*S. plan.*	*S. part.*	*S. var.*	*n*
1	≈25										
Transect I		79	186	96	23	41	32	82	12	6	182
Transect II		89	241	100	75	17	12	75	25	<1	287
Transect III		90	202	78	45	33	15	82	16	2	222
2	0.12	100	165	97	151	100	13	50	46	4	322
3	0.07	96	103	74	139	100	11	47	48	5	213
4	0.03	91	54	100	22	100	7	63	29	8	78

* Rounded to whole numbers.
† Reef 1 = total population; reefs 2–4 = adults only.
‡ *S. plan.* = *Stegastes planifrons; S. part.* = *S. partitus; S. var.* = *S. variabilis.*

that assessed the effects of this manipulation on *S. partitus*. However, *S. variabilis* characteristically has large territories (e.g., Gronell 1980) and occurs at much lower densities than either *S. partitus* or *S. planifrons*. Only 12 replicates were used for analyses of this species' response to the removal of *S. planifrons*, as one reef in each of the other four replicates seemed too small to support even one adult of *S. variabilis*.

Dynamics of recruitment and adult populations of Stegastes partitus

In San Blas, pelagic larvae of *S. partitus* settle onto reefs around new moon (Robertson 1992). Early recruitment was monitored by making full-moon censuses of recruits-of-the-month at 17 sites scattered over a ≈3 km^2 area (for methods see Robertson 1992, Robertson et al. 1993). Those sites included 11 plots on large reefs and the fringes of six entire patch reefs on which adult population dynamics also were monitored. I used those census data to estimate how annual recruitment levels varied over 11 yr (1983–1993), including the 6-yr experimental period, and the preceding 5 yr. Censuses of the 11 plots began in 1983, and of the six reefs in 1984.

The 17 recruitment sites varied in both size and habitat structure. Hence I could not use change in recruit densities to estimate fluctuations in recruitment. Instead I weighted data from all sites equally by scaling each year's recruitment level from a site as a percentage of the maximum annual level for that site, and used the mean of each year's set of percentage values as an estimate of that year's level of recruitment to the reef system as a whole. Maximum annual recruitment levels ranged from 20 to 434 ($\bar{X}$ = 98) fish at the 17 different sites.

Adult populations of *S. partitus* were censused annually on six isolated patch reefs. Because those reefs varied in size and habitat structure, I used the same weighting method as with recruitment (i.e., scaling each year's population size as a percentage of maximum population size for that reef) when estimating interannual variation in adult abundance in the study area. Maximum adult population size ranged from 20 to 160 ($\bar{X}$ = 89) fish on the different reefs.

RESULTS

Overlap in habitat use between Stegastes planifrons *and its congeners*

Most of the populations of *S. planifrons* and *S. partitus* on each of three shallow, emergent patch reefs and one large emergent reef in deep water were on the shallow reef slope (Table 2). Most *S. variabilis* on the large reef were in deeper habitat than that occupied by *S. planifrons*, although moderate numbers co-occurred with *S. planifrons*. All *S. variabilis* on the three shallow patch reefs were on the reef slope with *S. planifrons*. *S. planifrons* was the commonest of those three species in that reef slope habitat and *S. variabilis* the least abundant (Table 2).

S. planifrons, S. partitus, and *S. variabilis* were present on all 40 removal and control reefs and were the commonest species in the premanipulation populations: *S. planifrons* represented 56.3%, *S. partitus* 31.5%, and *S. variabilis* 10.4%, respectively, of 3003 individuals of six *Stegastes* species on those reefs (see also Table 1). *S. dorsopunicans* was present on 35% of those reefs and represented 5.8% of all individuals. *S. diencaeus* and *S. leucostictus* were present on 20 and 45%, respectively, of the 40 experimental reefs, but each represented <1% of all *Stegastes* individuals. The latter two species were absent from the reef-slope portions of the transects on the emergent large reef, and from the reef slopes of the three emergent patch reefs.

S. planifrons *removal experiment*

Change in abundance of S. partitus *and* S. variabilis.—After the removal of *S. planifrons*, the density of *S. partitus* increased on almost all the removal reefs but only about half the control reefs (Fig. 1). Both total and adult densities of *S. partitus* increased more on the removal reefs than on their paired control reefs following the removal of *S. planifrons* (Fig. 2). Within 1 yr after the removal of *S. planifrons* the density of adult

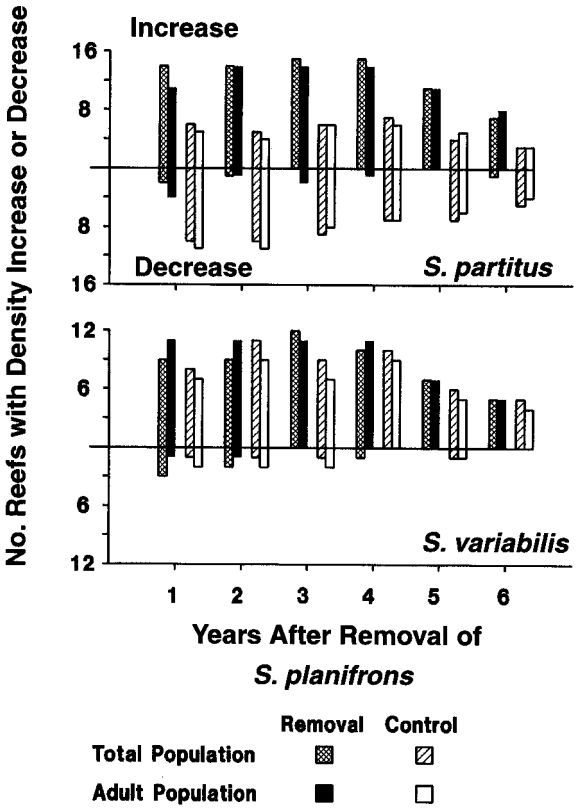

FIG. 1. Numbers of removal and control reefs on which populations of *Stegastes partitus* and *S. variabilis* increased or decreased (relative to their premanipulation state) after the removal of *S. planifrons*.

S. partitus on the removal reefs had increased by ≈50% (median net increase = 0.11 fish/m^2, median preremoval density = 0.20 fish/m^2; Fig. 2). Those increases persisted and continued until they leveled off 4 yr after the removal, at ≈160% above the preremoval density (median net increase on removal reefs = 0.32 fish/m^2 for years 4–6; Fig. 2). Over all years, the median levels of increase by both total and adult populations of *S. partitus* were ≈100% on the removal reefs, and about zero on the control reefs (Table 3).

Total and adult populations of *S. variabilis* increased on most of both the removal and control reefs after the removal of *S. planifrons* (Fig. 1). However, densities of adults of *S. variabilis* increased more on the removal reefs than the control reefs (Fig. 3). Those differences were established within 1 yr of the initial removal, at ≈50% above the preremoval state (medians of 0.15 fish/m^2 and 0.10 fish/m^2, respectively). They leveled off after 3–4 yr at ≈100% above the preremoval density (median net increase = 0.10 fish/m^2 for years 4–6; Fig. 3). The relative increases on the removal reefs were maintained throughout the experiment. There was a statistically nonsignificant tendency for total population densities of *S. variabilis* to increase more on removal reefs than on control reefs (Fig. 3). Overall, adult populations of *S. variabilis* increased by an median of ≈100% more on the removal reefs than on control reefs (Table 3). The increases in density by adults of *S. variabilis* on the removal reefs were smaller than those by adults of *S. partitus* (Figs. 3 and 2: median levels of net increase over years 1–6 were 0.09 adults/m^2 and 0.23 adults/m^2, respectively). There was considerable variation among replicates in the levels of increase in density by both *S. partitus* and *S. variabilis* separately and in combination (Figs. 2 and 3, Table 3).

The overall increase in the combined density of *S. partitus* plus *S. variabilis* was about half the premanipulation density of adults of *S. planifrons* on the removal reefs (Table 3). On the control reefs the median change in combined density of those two species was close to zero, and maximum increases were one-half to one-third the size of those on the removal reefs (Table 3). When population increases on the removal reefs reached their maximum extent, 4–6 yr after the removals, the combined density of adults of *S. partitus* plus *S. variabilis* had increased by ≈70% of the premanipulation density of *S. planifrons* (medians = 0.42

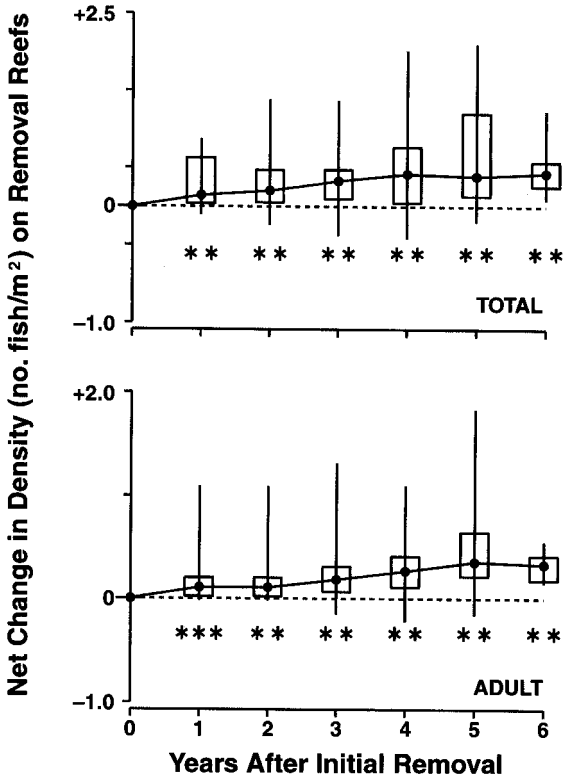

FIG. 2. Relative change in total and adult densities of *Stegastes partitus* on removal vs. control reefs following the removal of *S. planifrons*. Net change = [change in density on a removal reef, i.e., density in year X − premanipulation density in year 0] − [change in density on its paired control reef over the same period]. Plots show medians with quartiles and ranges. Wilcoxon paired-sample tests (one-tailed). *** $P < 0.001$, ** $P < 0.01$. Sample sizes: $n = 16$ for years 1–4, $n = 11$ for year 5, $n = 8$ for year 6.

TABLE 3. Levels of change in densities of *S. partitus* and *S. variabilis* following the removal of *S. planifrons*.

	Median (range) percentage change per replicate†	
	Removals	Controls
Change in density of *S. partitus* as % of its premanipulation state		
Adults + juveniles	+85 (−3 to +680)	−3 (−58 to +550)
Adults only	+110 (−25 to +380)	−5 (−70 to +400)
Change in density of *S. variabilis* as % of its premanipulation state		
Adults + juveniles	+93 (−31 to +716)	+33 (−20 to +137)
Adults only	+153 (−8 to +880)	+34 (−80 to +120)
Change in density of *S. partitus* plus *S. variabilis* as percent of premanipulation density of *S. planifrons*		
Adult + juveniles	+53 (+8 to +130)	+9 (−20 to +66)
Adults only	+59 (+16 to +193)	+3 (−30 to +63)

† When the premanipulation density was zero, each individual added represented a 100% increase. Datum for each replicate is the mean of changes for all (4–6) years. Sample sizes: change in density of *S. partitus* alone: $n = 16$; change in density of *S. variabilis* alone: $n = 12$; change in density of *S. partitus* + *S. variabilis*: $n = 16$.

fish/m^2 and 0.59 fish/m^2, respectively). Because adults of *S. partitus* and *S. variabilis* were smaller than those of *S. planifrons* (see *Materials and Methods*) increases in the combined biomass density of adults of *S. partitus* plus *S. variabilis* on the removal reefs probably averaged < 40% of the premanipulation biomass density of *S. planifrons* adults on those reefs.

Increases (averaged over all years) in the combined densities of *S. partitus* plus *S. variabilis* adults on the removal reefs were positively correlated with the preremoval densities of adults of *S. planifrons* on those reefs (Fig. 4; Pearson $r = 0.76$, $P = 0.001$). Density increases by *S. partitus* adults alone on the removal reefs also were correlated with the preremoval densities of *S. planifrons* adults (Pearson $r = 0.65$, $P = 0.007$). There was no correlation between analogous changes in combined densities of adults of those two species and changes in the density of *S. planifrons* on the control reefs (Pearson $r = 0.11$, $P = 0.34$). Absolute changes in adult *S. planifrons* densities were smaller on the control reefs (median = 0.17 fish/m^2, range = 0.01–0.43) than on the removal reefs (median = 0.60 fish/m^2, range = 0.14–1.41). There was a statistically

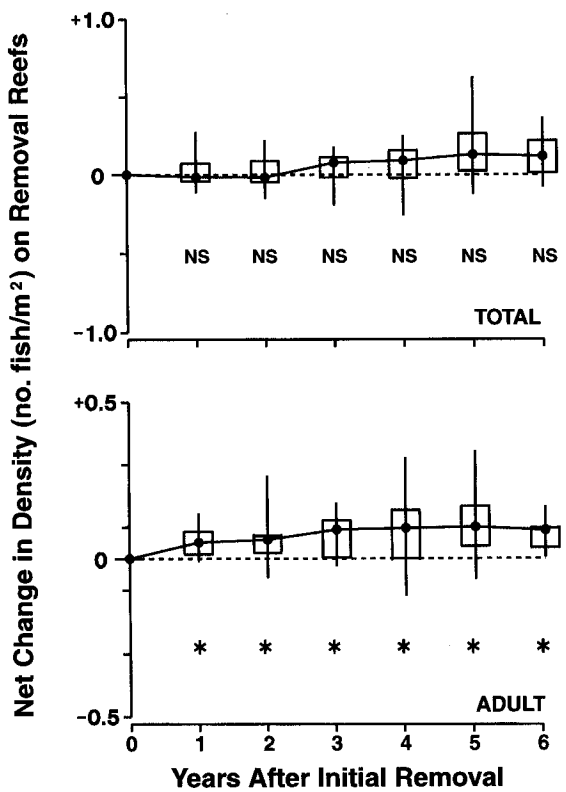

FIG. 3. Change in total and adult densities of *Stegastes variabilis* on paired removal and control reefs following the removal of *S. planifrons*. Plots show medians with quartiles and ranges. *$P < 0.05$, NS $P > 0.05$. Sample sizes: $n = 12$ for year 1–year 4, 9 for year 5, and 5 for year 6.

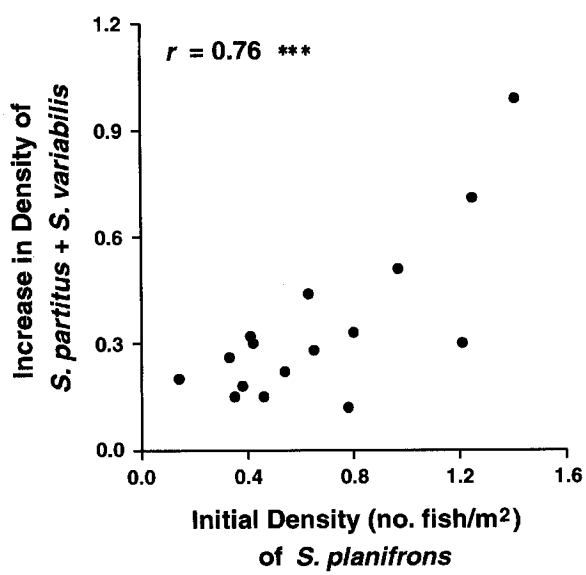

FIG. 4. Relationship between the level of increase in the adult population density (no. fish/m^2) of *Stegastes partitus* plus *S. variabilis* on a removal reef vs. the preremoval density of adults of *S. planifrons* on the same reef. $n = 16$; Pearson r, *** $P = 0.001$.

TABLE 4. Population responses by *Stegastes leucostictus* and *S. diencaeus* to the removal of *S. planifrons*.

Species	Population change	No. replicates with different population changes	
		Removals	Controls
S. diencaeus	Increase	3	2
	Decrease	0	1
	(Never present)	(13)	(13)
S. leucostictus	Increase	2	9
	Decrease	2	1
	(Never present)	(12)	(6)

nonsignificant, negative relationship between changes in the densities of adults of *S. partitus* and of *S. variabilis* on the removal reefs (Pearson $r = -0.36$, $P = 0.23$).

Both *S. diencaeus* and *S. leucostictus* remained rare on the experimental reefs after the removal of *S. planifrons,* and neither species showed any tendency to increase more on the removal reefs than on the controls (Table 4).

Change in microhabitat use by S. partitus.—Prior to the removals of *S. planifrons,* about half the adults of that species were in the centers and half at the edges of both removal and control reefs, whereas the great majority of adults of *S. partitus* were located at the edges of those reefs (Fig. 5; Wilcoxon paired-sample tests: *S. partitus* vs. *S. planifrons*; $P = 0.001$ for both removal and control reefs). Adults of *S. partitus* were much more abundant in central positions on the removal reefs at the end of the experiment than before *S. planifrons* was removed (Fig. 5, Wilcoxon paired-sample test, $P = 0.001$), while there was no change evident in their positions on the control reefs (Fig. 5; Wilcoxon paired-sample test, $P = 0.21$).

S. partitus *removal experiment*

Populations of *S. planifrons* showed no tendency to increase following the removal of *S. partitus,* and, if anything, decreased on removal reefs relative to the controls (Fig. 6). Populations of *S. variabilis* showed no consistent difference in patterns of change on the removal and the control reefs (Fig. 7).

Population and recruitment dynamics of Stegastes partitus

From 1983 to 1993 the adult population of *S. partitus* in the study area gradually increased to nearly twice its initial size (Fig. 8). However, during the period when experimental populations of *S. partitus* were responding to the removal of *S. planifrons* (i.e., 1988–1993) average adult population size in the study area at large was only about one-third greater than the average size before the experimental manipulations were started (1983–1987).

Annual recruitment levels of *Stegastes partitus* varied relatively little (maximum 2.1-fold) from 1983 to 1993 (Fig. 8). During most of the 6 yr (1987–1992) in which recruits were entering the experimental populations and affecting their adult component, the level of recruitment was low compared to levels either during the previous 4 yr (1983–1986) or immediately afterwards (1993).

DISCUSSION

Effects of interspecific competition on abundance and microhabitat use of the study species

When *Stegastes planifrons* was nearly eliminated from habitat in which it was the most abundant territorial damselfish, four of its congeners responded as follows: (a) there was a doubling in the adult densities of *S. partitus* and *S. variabilis,* and total density of *S. partitus*; (b) adult populations of *S. partitus* plus *S. variabilis* (and of *S. partitus* alone) increased most where *S. planifrons* previously had been most dense; (c) population increases by *S. partitus* and *S. variabilis* were established within 1 yr and were persistent, but took ≈4 yr to reach their maximum levels; and (d)

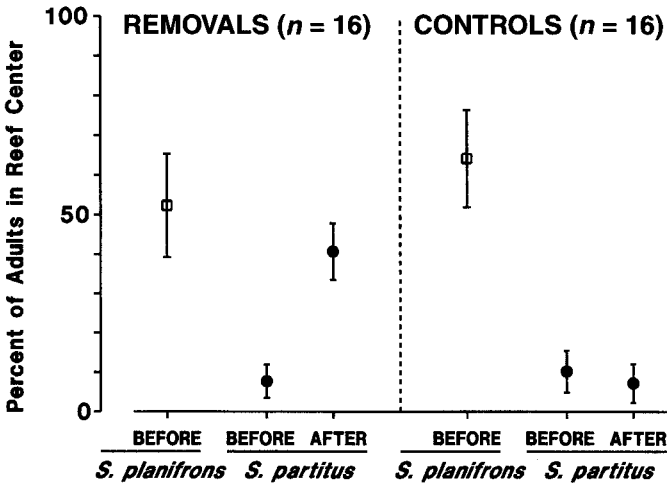

FIG. 5. Microhabitat use by *Stegastes planifrons* and *S. partitus.* Before = condition before removal of *S. planifrons,* After = condition 4–6 yr after the removal at the end of the experiment. Plots show means with 95% confidence intervals. Wilcoxon paired-sample tests (one-tailed) comparing percentages of two populations in reef centers. *S. planifrons* vs. *S. partitus* on same reef before experimental manipulation of *S. planifrons* (removal reefs $P < 0.001$, control reefs $P < 0.001$); *S. partitus* on the same reef before vs. after experimental manipulation of *S. planifrons* (removal reefs $P = 0.001$, control reefs $P = 0.21$). $n = 16$ reefs of each type.

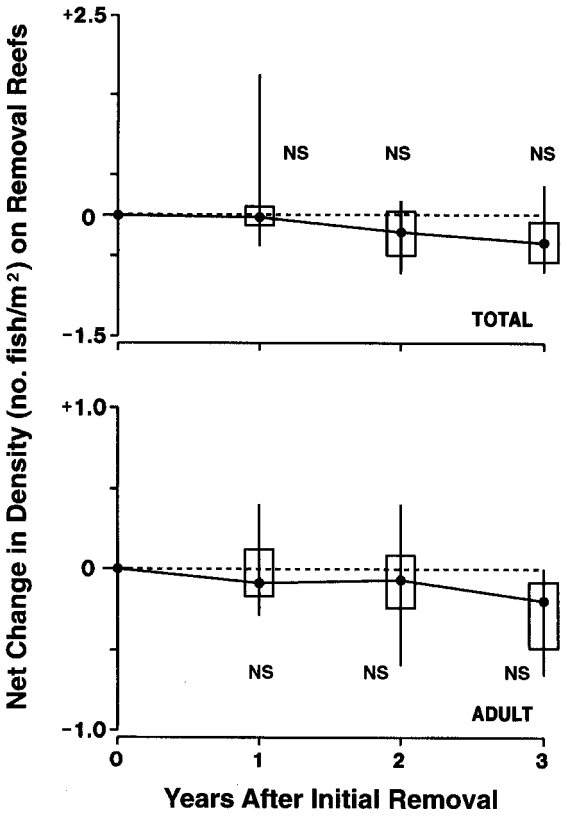

FIG. 6. Change in total and adult densities of *Stegastes planifrons* on paired experimental and control reefs following the removal of *S. partitus*. Plots show medians with quartiles and ranges. NS indicates $P > 0.05$. $n = 8$ for all years.

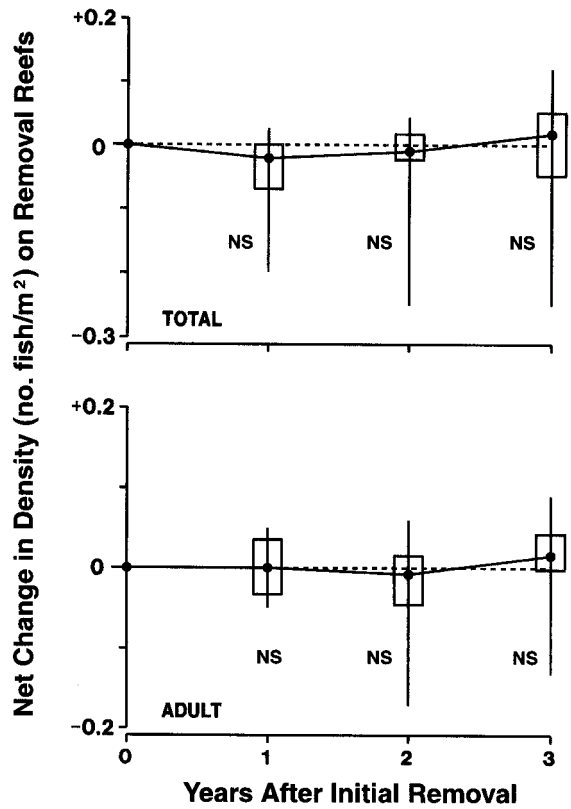

FIG. 7. Change in total and adult densities of *Stegastes variabilis* on paired experimental and control reefs following the removal of *S. partitus*. Plots show medians with quartiles and ranges. NS indicates $P > 0.05$. $n = 8$ for all years.

populations of *S. diencaeus* and *S. leucostictus* remained unchanged at very low levels. There was no numerical response by either *S. planifrons* or *S. variabilis* to the removal of *S. partitus*.

These results show that interspecific competition with the abundant, highly aggressive, and ecologically influential damselfish *Stegastes planifrons* in its primary habitat strongly and persistently limits the abundance of adults of the two most common co-occurring congeners in a density-dependent manner. Large experimental reductions in the density of *S. planifrons* were required to reveal this density-dependent relationship as those two species did not show a consistent numerical response to smaller natural changes in the density of *S. planifrons* on control reefs. Competition with *S. planifrons* does not appear to be responsible for the rarity of *S. diencaeus* and *S. leucostictus* in that habitat. While it is possible that competition with the increased populations of *S. partitus* and *S. variabilis* (i.e., competitive mutualism, McNally 1983) led to the lack of response by populations of *S. diencaeus* and *S. leucostictus*, that does not seem likely. The rarity of *S. leucostictus* in that habitat may be due to habitat preference (Wellington 1992), combined population and biomass densities of *S. partitus* and *S. variabilis* re-

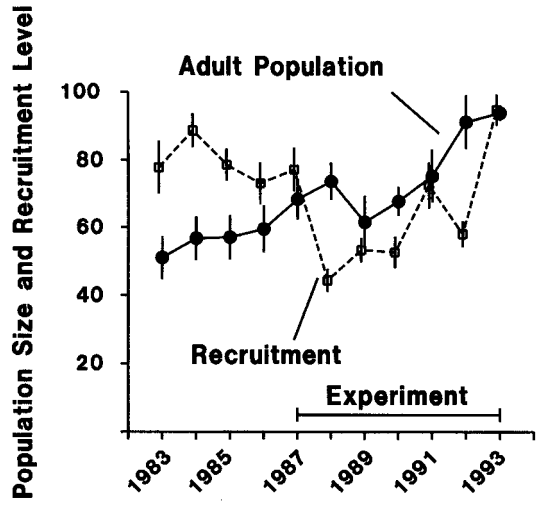

FIG. 8. Population and recruitment dynamics of *Stegastes partitus*. $n = 6$ reefs for adult populations and those reefs plus 11 plots for recruitment. Population and recruitment values are shown on the same scale (as a percentage of the maximum of each; see *Methods* for details). Plots show annual means with standard errors.

mained substantially below the preremoval densities of *S. planifrons,* and adults of *S. diencaeus* are competitively superior to those of smaller species (Robertson 1995).

The limiting effects of *S. planifrons* on the density of *S. partitus* are nonreciprocal. Hence the abundance and distribution patterns of these two species evidently are governed by an asymmetric competitive relationship and not by a competitive "lottery" (Sale 1974, 1977, Chesson and Warner 1981) among species that have equal abilities to hold space, and among which space is allocated on a first-come, first-served basis.

Although *S. partitus* evidently does not limit the abundance of *S. variabilis* there are indications that the reverse may occur, at least in the absence of *S. planifrons,* i.e., the weak negative correlation between levels of increase by those two species in the *S. planifrons* removal experiment. This possibility currently is being tested through experimental removals of *S. variabilis.*

While there were general abundance responses by *Stegastes partitus* and *S. variabilis* to the removal of *S. planifrons,* there was considerable spatial variability, and some species specificity, in the strength of those responses. A moderate amount of the spatial variation in response strength evidently was due to variation in the density of *S. planifrons.* Other contributing factors probably included spatial variation in habitat quality, in recruitment (cf. Doherty 1991), and in demographics (cf. Aldenhoven 1986, Eckert 1987, Fowler 1990). In addition, reefs in the study area have undergone marked habitat changes over the past decade, associated with substantial declines in coral populations and increases in macroalgal abundance (Ogden 1993, Shulman and Robertson, *in press*). Such changes noticeably altered habitat quality on some of the experimental reefs during the period of my study. Differences between the responses of *S. partitus* and *S. variabilis* included (a) smaller increases in absolute densities of *S. variabilis,* and (b) increases by *S. variabilis,* but not *S. partitus,* on both control and removal reefs. *S. variabilis* and *S. partitus* presumably have different degrees of overlap in resource requirements with *S. planifrons* and may have different intensities of behavioral (Myrberg and Thresher 1974, Sale et al. 1980, Harrington 1993) and population interactions. *S. partitus* is substantially smaller than both *S. planifrons* and *S. variabilis.* Such size differences are likely to affect the outcome of agonistic interactions and influence patterns of space allocation (Robertson 1984, 1995, Shulman 1985, Persson 1985, Brown and Maurer 1986) and the strength of population interactions. In addition, population densities of *S. variabilis* normally are much lower than those of *S. partitus* and may be more strongly limited by factors other than competition with *S. planifrons.*

Increases in the density of adults of *S. parititus* plus *S. variabilis* on the removal reefs reached only ≈70% of the population density and ≈40% of the biomass density that adult *S. planifrons* had prior to their removal. Similar failure of populations released from competition to equal their competitor's numeric and biomass densities has been observed in other experiments on competition (undercompensation, Schmitt and Holbrook 1990). Here it may have been due to differences in habitat preferences or territory size requirements, although insufficient recruitment by *S. partitus* and *S. variabilis* may also have been involved.

In its primary habitat *S. planifrons* occurs throughout a range of microhabitats, while the competitively inferior species, *S. partitus,* is restricted to one microhabitat. When released from competition with *S. planifrons, S. partitus* expands the range of microhabitats it uses. Here, reduced overlap in microhabitat use is a consequence of asymmetric interspecific competition that has strong, linked effects on the abundance of the subordinate species.

Trajectory of the compensatory response and its relation to background population and recruitment dynamics

The speed, persistence, and magnitude of the density responses by *S. partitus* and *S. variabilis* to the removal of *S. planifrons* indicate that *S. planifrons* normally has an ongoing, strong limiting effect on those species, i.e., that competition between them is persistent rather than intermittent (cf. Schoener 1983). That the compensatory response by the population of *S. partitus* took ≈4 yr to reach its maximum extent may have been due in part to low juvenile recruitment during the early years of the experiment (Fig. 8). However, there also may be positive feedbacks during population increase, e.g., residents may attract conspecific recruits (cf. Sweatman 1988, Booth 1992), leading to enhanced local recruitment as populations rise due to increased survival in the absence of *S. planifrons.* Postrecruitment relocation of fish between reefs (cf. Robertson 1988*a,* 1989) may also have been involved.

Due to the ability of populations of long-lived species to "store" recruitment (Chesson and Warner 1981, Warner and Chesson 1985) it may be difficult to detect the influence of recruitment fluctuations on their population dynamics (Warner and Hughes 1988). However, *S. partitus* is relatively short lived. Maturity is reached in <1 yr, and the average adult is only ≈1 yr old, and has a half-life of ≈1 yr (D. R. Robertson and E. B. Brothers, *unpublished data*). Hence the relationship between interannual fluctuations in the abundance of adults of *S. partitus* and in its recruitment potentially could indicate the extent to which its population dynamics are controlled by recruitment dynamics. Since the gradual increase in the abundance of adults of *S. partitus* from 1983 to 1993 was not associated with a similar trend in recruitment, its population dynamics evidently are not recruitment driven. The fact that recruitment occurred at relatively low levels during most of the experimental period indicates that competitive limitation of populations of *S. partitus* by *S. planifrons*

is not an infrequent event restricted to periods of unusually high recruitment. It is more likely that *S. partitus* normally is close to saturating the parts of the primary habitat of *S. planifrons* that the latter does not occupy. The long-term, natural population increase by *S. partitus* may be a response to long-term changes in habitat quality and hence in habitat availability for it or its congeners.

The duration of experiments on density compensation

One of the problems that faces ecologists is deciding how long it is necessary to run experiments that aim to assess the extent of a compensatory response by a population following its release from competition. Short-term responses often are not good predictors of overall demographic effects and responses may need time to stabilize (Yodzis 1988, Schmitt and Holbrook 1990, Gurevitch et al. 1992). There may be reversals in competitive effects over time (Connell 1983), or competition may occur only intermittently as a result of fluctuations in resource abundance (Schoener 1983, Schmitt and Holbrook 1986). In tropical reef fishes, as with many marine organisms that have open populations, there often are substantial interannual fluctuations in recruitment of pelagic juveniles (e.g., Sale et al. 1984, Doherty 1991). Like resource fluctuations, those recruitment fluctuations may affect the temporal patterning of intraspecific competition (Jones 1990). Experiments on density compensation by such organisms will need to be of sufficient duration to accommodate the potential for interannual fluctuations in recruitment to produce intermittent interspecific competition.

Yodzis (1988) suggested two generations as a suitable temporal scale for experiments on population responses to competition. In my study it took about four generations for *S. partitus*' population to achieve its maximum compensatory response. The fact that the response had stabilized only became evident when the population trajectory spanning 6 yr and six generations became available. That 6-yr period also is about the time taken for one population turnover, which Connell and Sousa (1983) proposed as an appropriate minimum scale for assessing population stability. That entire period also was necessary to show the relationship between the response to competitive release and both recruitment dynamics and background fluctuations in adult abundance.

In the only other experiment on reef fishes analogous to my study, Schmitt and Holbrook (1990) maintained the removal treatment for 4 yr, or a little over one generation. Density increases at the end of that time were smaller than predicted. It was unclear whether population responses had stabilized by then, because they examined them only twice, immediately after the removal and 4 yr later, and lacked a response trajectory. Unlike most reef fishes, their study species were livebearers with self-recruiting, closed populations. Density compensation could proceed rapidly to stabilization in a closed population if increased reproduction occurred in response to release from competition (cf. Thresher 1985). In open populations trajectories of compensatory responses are likely to be more variable, because recruitment of pelagic juveniles into the released population will fluctuate independently of local reproductive and demographic responses to release from competition. Hence it is important that response trajectories be regularly monitored, to determine if, when, and at what level they stabilize. Under most conditions, minimum time scales for experiments on density compensation by marine species that produce pelagic juveniles seem likely to be on the order of several generations for long-lived forms, or several years (i.e., several recruitment seasons) for short-lived ones, and to be strongly dependent on the nature of ongoing background population and recruitment dynamics. Often it may not be possible to decide on a appropriate time scale before starting the experiment.

Interspecific competition and habitat use: patterns of association among reef fishes?

Interspecific competition generally is associated with high overlap in diet and microhabitat use (Schoener 1983), although patterns of habitat use may not be good predictors of the actual occurrence of such competition (Holbrook and Schmitt 1989). Is there any relationship between patterns of habitat use and the occurrence of interspecific competition among ecologically similar reef fishes? While *S. planifrons* strongly limits the abundance of two congeners that commonly co-occur in its primary habitat it has no apparent effect on two species that rarely occur there (this study). Doherty (1982, 1983) found a similar lack of effect by a West Pacific territorial damselfish, *Pomacentrus wardi,* on the abundance of juveniles of a rare species in *P. wardi's* primary habitat. *P. wardi* occurs at relatively low densities in that habitat [$\approx$0.2 adults/m^2 (Doherty and Fowler 1994*b*) vs. $\approx$1–2 adults/m^2 for *Stegastes* species in some habitats (this study, Robertson et al. 1981, Robertson 1984, 1995)] and its abundance appears to be largely unaffected by intraspecific competition (Doherty and Fowler 1994*b*). Hence the virtual absence of other ecologically similar damselfishes from *P. wardi*'s primary habitat (Robertson and Lassig 1980, Sale et al. 1980) seems likely to be due to their habitat preferences rather than to competition with *P. wardi.* Wellington's (1992) data indicate that macrohabitat segregation by *S. leucostictus* and *S. variabilis* arises from differences in habitat preferences of recruits and older juveniles. While two surfperches studied by Schmitt and Holbrook (1990) limit each other's abundance in shared habitat, habitat preference is responsible for the absence of one species in unshared habitat. Larson (1980) concluded that macrohabitat segregation by two territorial rockfishes is influenced mainly by habitat preferences, which are reinforced by interspecific dif-

ferences in dominance ability. In sum those data indicate that interspecific competition can have strong effects on abundances of species in shared habitat, but that habitat preferences may be the primary factor responsible for macrohabitat segregation. If this is a general pattern it could be useful for assessing the potential importance of interspecific interference competition among reef fishes.

Potential importance of interspecific competition for populations of Stegastes *species*

How important might interspecific competition be for the overall abundances of the six members of the *Stegastes* guild on the reef system of San Blas Point, assuming that any competition among congeners is largely restricted to shared habitat? Although both *S. partitus* and *S. variabilis* have habitat refuges, in which each is virtually the only species present, together those refuges occupy <20% of the fringes of the several hundred reefs in that 15-km^2 reef system. The remainder of the shallow sides of reefs consists of habitats occupied primarily by *S. planifrons* and/or *S. dorsopunicans* (D. R. Robertson, *personal observations*). Thus competition with *S. planifrons* (and *S. dorsopunicans*?) on reef fringes probably does have a substantial effect on the overall abundances of *S. partitus* and *S. variabilis* in that reef system. Most *S. dorsopunicans* live in extensive areas of refuge habitat on the semiemergent tops of reefs (Waldner and Robertson 1980, Robertson 1995; D. R. Robertson, *personal observations*), and *S. planifrons* is competitively dominant over the main species that co-occur in its primary habitat (this study). Hence interspecific competition seems unlikely to have much effect on overall abundances of either of those two species. *S. diencaeus* shares its primary habitat with several congeners, which actually outnumber it in that habitat. Although adults of *S. diencaeus* are competitively dominant in that habitat (Robertson 1995), interactions with co-occurring congeners could affect its juveniles and hence its abundance. *S. leucostictus* has a habitat refuge (Waldner and Robertson 1980). However, a large proportion of its population extends into contiguous habitat where congeners also commonly occur (D. R. Robertson, *personal observations*). Because *S. leucostictus* is a small species it seems unlikely to have any competitive advantage and has the potential to be strongly affected by interspecific competition with congeners. Thus competition with congeners likely has no significant effect on the overall abundances of two species of *Stegastes,* probably does substantially limit two species, and potentially could have major effects on the abundances of two others.

Effects of interspecific competition among other reef fishes

What do the available data show about effects of interspecific competition among other reef fishes? Existing information about such competition almost exclusively concerns aggressive, site-attached species (but see Thresher 1985). Doherty (1982, 1983) found that one territorial damselfish in its primary habitat did not reduce the recruitment and juvenile survivorship of an uncommon congener, but did limit the total abundance of one of five taxa of other herbivorous fishes. Jones (1987*a,* 1988) showed that adults of two planktivorous damselfishes limited the recruitment of confamilial heterospecifics in one of four cases, but did not affect the survival or growth of each other's juveniles. Sweatman (1985) worked with four planktivorous damselfishes (including one species studied by Jones) and found that the two species that are sedentary and aggressive reduced larval recruitment of heterospecifics in 12 of 27 cases. Shulman et al. (1983) found that recruitment of both of two taxa of heterospecifics was reduced by adults of *Stegastes leucostictus.* Thus interspecific competition at least occasionally limits recruitment of reef fishes. Whether such limitation carries through to affect adult abundances has yet to be assessed through experiments.

All of six experimental studies on territorial reef fishes have found that interspecific interactions affect local-scale habitat use (Hixon 1980, Larson 1980, Ebersole 1985, Robertson and Gaines 1986, Clarke 1989, Schmitt and Holbrook 1990). Interspecific territoriality occurs in various major trophic and taxonomic groups of tropical reef fishes, e.g., corallivorous and omnivorous chaetodontids (Roberts and Ormond 1992); herbivorous pomacentrids (Sale 1974, 1977, Doherty 1982, 1983, Robertson 1984), and acanthurids (Robertson and Gaines 1986); planktivorous pomacentrids (Sweatman 1985, Jones 1987*a, b*) and chaenopsids (Clarke 1989); and benthic-feeding carnivorous serranids (Pressley 1981, Shpigel and Fishelson 1989). The asymmetry in the competitive relationship between *S. planifrons* and *S. partitus* follows a general pattern (Schoener 1983, Persson 1985, Brown and Maurer 1986)—a large, pugnacious species socially and competitively dominates a smaller, less aggressive one. Similar size and/or behavioral asymmetries occur among other territorial reef fishes (e.g., Robertson and Gaines 1986). Weaker asymmetries in the effects of competition among reef fishes are associated with similarities in body size and less well-defined differences in social dominance ability (Larson 1980), and with the involvement of exploitative competition (Schmitt and Holbrook 1990). Interspecific interference competition among species with unequal competitive abilities clearly has the potential to have stronger effects on both the distribution and abundance of tropical reef fishes than is currently appreciated. Generalizations about the relative influence of inter- and intraspecific competition on the abundances of such fishes will only become possible through experimental studies that examine effects of competition in relation to long-term population and recruitment dynamics and that system-

atically assess relationships between those effects and factors such as patterns of habitat use, the presence and form of resource defense, the degree of asymmetry in competitive ability, types of food resources, population density, and demographic characteristics.

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