POPULATION DYNAMICS AND RESOURCE UTILIZATION BY THE DUSKY
DAMSELFISH, *Stegastes adustus* (Troschel, 1865)

by

Glauco A. Rivera Betancourt

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Approved by:

_____   _____
Edgardo Ojeda Serrano, Ph.D.   Date
Member, Graduate Committee

_____   _____
Alberto M. Sabat, Ph.D.   Date
Member, Graduate Committee

_____   _____
Ernest H. Williams, Ph.D.   Date
Member, Graduate Committee

_____   _____
Jorge R. García Saís, Ph.D.   Date
President, Graduate Committee

_____   _____
Allen R. Lewis, Ph.D.   Date
Representative of Graduate Studies

_____   _____
Nilda E. Aponte, Ph.D.   Date
Chairperson of the Department

RESUMEN

Los peces del arrecife de coral dependen del sustrato del arrecife a lo largo de su vida por lo que los patrones de distribución y abundancia pueden estar regulados por esa asociación. La variabilidad espacio-temporal en la abundancia de la damisela, *Stegastes adustus*, fue estudiada en el sistema de arrecifes de coral en La Parguera, suroeste de Puerto Rico. Durante un año se condujeron observaciones mensuales sobre transectos permanentes establecidos en la sección frontal de cinco arrecifes. Las asociaciones con el microhabitáculo se evaluaron mediante la relación del sustrato disponible y la abundancia de los peces y mediante la relación de la composición del territorio y la cantidad de peces con territorio establecido. En adición se llevó a cabo experimentación multifactorial de manipulación de sustrato combinando la presencia y ausencia de refugio y alimento. Se observó un aumento en la abundancia de *S. adustus* en comparación con datos de abundancia previo a las reducciones en las poblaciones de *Acropora* spp. y *Diadema antillarum*. El arrecife más somero demostró una abundancia significativamente más alta y se obtuvo un pico estacional en dos arrecifes. Los resultados coincidieron con datos reportados para otras áreas del Caribe. Los juveniles y adultos demostraron abundancias significativamente diferentes dentro y entre etapas ontogenéticas. La cantidad de territorios de damiselas resultó estadísticamente igual entre todos los arrecifes y se asoció a la abundancia promedio, excepto en el arrecife más somero. El sustrato firme consolidado dominó la cobertura de sustrato arrecifal en todos los arrecifes, sin embargo la abundancia de damiselas

no se relacionó a este sustrato en particular, pero sí a otros tipos de sustratos con menor cobertura. Aunque *Montastraea anularis* fue el coral con mayor cobertura, no se obtuvo una relación que influyera en la abundancia de las damiselas. La cantidad de territorios encontrados se relacionó con la cobertura por coral muerto. La rugosidad, similar entre todos los arrecifes no tuvo ningún efecto sobre la abundancia. Una vez un área de sustrato es ocupada por las damiselas reclutas, la selección de microhabitáculos puede explicar la abundancia y distribución de juveniles y adultos. La investigación sugiere que *S. adustus* es una especie oportunista generalista que se asienta y recluta en un hábitat específico pero que se beneficia al modificar su entorno una vez se torna juvenil y alcanza la adultez. No empece a la variabilidad del asentamiento, factores ambientales en conjunto con procesos biológicos y ecológicos podrían explicar las diferencias observadas en la abundancia y distribución de *S. adustus*.

ABSTRACT

Coral reef fishes depend upon the reef substrate for the duration of their lives. Consequently, patterns of distribution and abundance of reef fishes may be influenced by this relationship. The spatial and temporal abundance variability of the dusky damselfish, *Stegastes adustus* was studied in the coral reef ecosystem of La Parguera, southwestern Puerto Rico. Monthly surveys were conducted over one year at permanent transects established in the fore reef areas of five reefs. Microhabitat association was evaluated by correlating the quantified available substrate in transects and within territories to fish abundance and the number of fish with territories respectively, and by multi-factorial manipulative experiments combining the presence and absence of refuge and food. An increased abundance of *S. adustus* was noted when compared to that recorded prior to the decline of *Acropora* spp. and *Diadema antillarum*. Significantly higher abundance was observed in one relatively shallower reef and a seasonal peak in abundance was recorded for two reefs. These results corresponded with observations elsewhere in the Caribbean. Juveniles and adults showed significant differences in abundance between and within ontogenetic stages. The amount of dusky damselfish territories was similar among reefs and was correlated to mean fish abundance, except in the shallower reef. Turf colonized pavement dominated the reef substrate at all sites. Fish abundance was not correlated to this particular substrate type but to lesser substrate categories. Regardless of the higher cover by boulder star coral, *Montastraea annularis* no correlation was found between the coral species and fish abundance. The

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number of established territories was related to substrate cover by dead coral.

Rugosity was similar between reefs but did not influence abundance. Choice of

microhabitat during recruitment may explain abundance and distribution of

juveniles and adults once a substrate section is occupied by the fish. This study

suggests that *S. adustus* is an opportunistic generalist that settles and recruits to

a specific habitat but that juveniles and adults may further benefit from modifying

their surroundings. Setting aside variability in settlement, environmental factors

and other biological and ecological processes may explain the observed

differences in the abundance and distribution of *S. adustus*.

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DEDICATION

I dedicate this work to my beloved wife and two boys, Elga Enid, Glauco and Carlos; to my parents, Glauco and Vivian; and to my parents-in-law, Carlos and Célida, for their support and encouragement during all these years.

To the memory of Dannie, from eternity you still are part of my committee.

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INTRODUCTION

Coral reefs are confronting a global crisis (Bellwood et al. 2004; Hughes et al. 2003; Pandolfi et al. 2003). Throughout the tropics, reefs that previously were dominated by scleractinian corals are experiencing a phase shift toward algal communities, affecting reef fish assemblages (Jones et al. 2004). Caribbean coral reefs have experienced wide spread degradation in the past decades, mostly from anthropogenic sources such as oil pollution, sewage discharge, sedimentation caused by upland vegetation clearing, anchoring, ship grounding, and global warming (Bellwood et al. 2004; Goenaga 1990; Hughes 1994; Hughes et al. 2003; Jackson et al. 2001).

The degradation of coral reefs would have serious ecological implications for coral reef fishes. Conversely, reef fishes may play a role in this degradation as some omnivorous species remove live coral tissue when cultivating algal turf for grazing within their territories. The balance of such an interaction merits attention when considering aspects of coral reef conservation.

Two major ecological events affecting Caribbean coral reefs have influenced the behavior, abundance and distribution of coral reef fishes. These include the mass-mortality of a key herbivore, the long-spined sea urchin *Diadema antillarum* in 1983-1984 (Lessios et al. 1984) and the regional decline of *Acropora palmata* and *A. cervicornis* in 1982-1984 (Aronson and Precht 2001; Precht 2002). *Stegastes planifrons* was observed to display an aggressive territorial behavior in defense of food resources against *D. antillarum* (Williams 1979). The algal increase experienced in Caribbean reefs after the

disappearance of the long-spined sea urchin allowed an increase in abundance of herbivorous fishes because of lack of competition for algal food resources (McClanahan 1994; McClanahan et al. 1996). Meanwhile, the high topography and spatial complexity and the surface area provided by standing live and dead *Acropora palmata* benefited territorial damselfishes in terms of refuge and abundance (Lirman 1999), but at an adverse cost for live coral due to "farming" by the damselfishes (Potts 1977).

Intense artisanal fishing pressure in worldwide tropics led to overfishing of several slow-growing target species, most of which are piscivores (e.g., large serranids and lujtanids). This situation was reported occurring in the Caribbean by Hawkins and Roberts (2004), in which artisanal fishing affected fish assemblages and benthic habitats. The decline of large diurnal reef piscivores resulted in a relative dominance of herbivores of different taxonomic groups (McClanahan 1994, McClanahan et al. 1996). As a consequence, the coral reef fish community structure has been beneficially influenced by removal of natural predators of reef fishes. This scenario boosted the increase in abundance, expanded the distribution, and increased longevity of prey damselfishes because of low competition and predation (Almany 2004a; Carr and Hixon 1995; Hixon and Beets 1993).

Aquarium trade of ornamental fishes is an increasing industry focused on the capture of several target coral reef fish species (Sadovy 1992; Sadovy and Vincent 2002). This practice may jeopardize many of the overlooked fish species

by ecologists. Sedentary species, like damselfishes, are vulnerable, easily and efficiently collected.

Three major taxonomic groups comprise the main coral reef fish assemblage (Choat and Bellwood 1991), these are the chaetodontids (Chaetodontidae, Pomacanthidae), the acanthuroids (Acanthuridae, Siganidae, Zanclidae) and the labroids (Scaridae, Pomacentridae, Labridae). This group of demersal fishes remains strongly associated to the coral reef throughout most of their juvenile and adult life history stages (Choat and Bellwood 1991). The pelagic planktonic larval phase is the only non-reef related stage (Leis 1991) in their two-phase life history cycle. Reef fishes are closely linked to the substratum, hence individual use of microhabitat is one factor that can influence fish distribution in small spatial scales. Jones (1991) emphasized on territoriality, age distribution, and habitat quality as factors influencing space resource use by coral reef fishes. Substratum is generally considered to be important in providing shelter from predators, nesting sites, and food resources (Tolimieri 1998). An increase in the number of shelter sites results in a rise of the number of reef fish recruits (Shulman 1984).

The family Pomacentridae includes four marine genera and 14 Caribbean species: *Abudefduf* (2 spp.), *Chromis* (5 spp.), *Microspathodon* (1 spp.), and *Stegastes* (6 spp.). *Abudefduf* and *Chromis* maintain temporary territories, swim in groups and feed mainly in the water column immediately over the substrate, while *Microspathodon* and *Stegastes* are territorial bottom attached non-schooling individuals throughout the year (Itzkowitz 1977). Pomacentrids are the

smallest sized herbivorous fishes (Choat 1991) and moderately long-lived

(Schwamborn and Ferreira 2002). Due to the sedentary behavior they depend

on substratum for refuge against predators, nesting, and feeding.

Six *Stegastes* species, commonly known as damselfishes, are present in

the Caribbean, *S. adustus*[1] Troschel, 1865 (Caribbean dusky damselfish) (Smith-

Vaniz et al. 1999), formerly treated as a senior synonym of *S. dorsopunicans*

Poey 1868; *S. diencaeus* Jordan and Rutter 1897 (longfin damselfish); *S. partitus*

Poey 1898 (bicolor damselfish); *S. variabilis* Castlenau 1855 (cocoa damselfish);

S. planifrons Cuvier 1830 (three-spot damselfish); *S. leucostictus* Müller and

Troschel 1848 (beaugregory).

Only *S. diencaeus*, *S. adustus* and *S. planifrons* farm and defend

permanent territories. Omnivore and herbivore damselfishes utilize coral

substrate to harvest an algal turf to supply a large portion of the dietary

requirements. The algal turf accumulates organic detritus, and also harbors

diatoms and bacteria (Choat 1991). Farming process involves nipping of coral

tissue to cultivate the alga (Kaufman 1977). These fishes are specific in terms of

habitat selection, preferring high quality territories. Characteristics of high quality

habitat are a complex spatial refuge and height above the ground, usually found

on *Montastraea* spp. and *Acropora* spp. complex (Tolimieri 1998; Itzkowitz 1977),

but high quality habitats are not always available. *Stegastes* was known to

associate mainly to *Acropora* prior to its decline and now may have shifted to

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[1] Latest scientific nomenclature provided by Nelson et al. (2004), will be followed throughout this study.

other coral species, particularly the *Montastraea annularis* species complex (Tolimieri 1995). Almany (2004a) demonstrated that 80% of new settlers in coral species other than *Acropora* were damselfishes when studying habitat complexity-reef fish relationships.

Jones (1990) suggests that population dynamics can be better assessed by a combination of experiments and parallel observations on undisturbed populations. The use of single factor experiments may lead to a misrepresentation of multifactorial causes controlling distribution and abundance patterns. Combined factors may exert a synergistic effect over fish populations not found when evaluating individual factors. Evaluation of patterns by implementing multifactorial manipulative experiments may lead to discovery of unmeasured but important factors contributing to the pattern (Jones 1988; Shima 2001). In order to identify primary factors, the fish population must be subdivided into homogeneous subunits (Jones 1991).

This will be the first study involving observational and experimental methods with any *Stegastes* species in Puerto Rico in approximately 25 years. On this research, I describe the abundance and distribution of populations of the Caribbean dusky damselfish, *Stegastes adustus* in coral reefs of La Parguera and evaluate if its abundance and spatial distribution are related to microhabitat characteristics that could regulate populations. Experimental evaluation of factors controlling these population attributes is necessary to manage fish communities, while knowledge of population structure is necessary to manage damselfishes, even when it sounds faintly ridiculous (Doherty 1991).

Results from this research may be applicable in the context of coral reef conservation and management. The outcome will help to determine whether fish species play an important role in structuring local coral reef communities, and to what extent Caribbean dusky damselfish may be exerting an adverse impact to coral species and coral reef health. A practical application of the understanding about habitat preferences is of major significance when, as an example, restoring coral reefs or designing and constructing artificial reef fish habitats, given that the new structure should provide reef fishes with similar characteristics and function of their natural habitat. These data will also serve as a baseline for comparisons to future changes in the abundance and distribution of *S. adustus* in La Parguera, southwestern Puerto Rico.

This dissertation is organized in a manuscript fashion. Chapter 1 is an evaluation of the spatial and temporal variations in the population of *S. adustus*, a characterization of the habitat and an evaluation of how benthic microhabitat resources were utilized and its relationship in patterns of abundance. Chapter 2 investigates how the distribution of recruits under specific factors might determine the distribution of juveniles and adults.

LITERATURE REVIEW

Coral reefs have a patchy distribution, leading to the assumption that associated reef fish communities are accordingly distributed on the large scale. But, what occurs to coral reef fishes within and among reefs of the same system? Coral reef fish communities are an open stochastic nonequilibrial assemblage (Sale 1991) affected by larval dispersion, settlement and postsettlement processes (Victor 1991; Doherty 1983; 1991; Jones 1991). Because recruitment is variable in space and time, the population structure may be affected by that variability (Jones 1990; Sale and Douglas 1984). A perspective that views marine populations, including fishes, as grouped into metapopulations has now become well established (Sale et al. 2006).

The influence of habitat, settlement, and post-settlement over recruitment success has been mostly studied for acanthurids, labrids and pomacentrids (Caselle and Warner 1996; Risk 1997; Robertson 1988; Shima 2001). Larval reef fishes return to the reef environment (i.e., pre-settlement connectivity) assisted by physical processes, such as tidal flows, internal waves, and wind driven currents (Cowen 2002; Cowen et al. 2000; Kingsford et al. 1991; Leis 1991; Mora and Sale 2002; Sponaugle and Pinkard 2004; Sponaugle et al. 2002), but late pelagic stages of coral reef fishes are capable of detecting reefs and swimming directionally towards them (Leis et al. 1996). Larvae make a final approach to the reef using a combination of different mechanisms (e.g., behavior, abilities, and sensorial cues) to actively search and select settlement sites. Fisher (2004) found that late post-larval pomacentrids spent most of their time in

the top two meters of the water column. The ability of the larval fishes to migrate vertically is relevant for finding and being able to settle on a reef. During settlement, fishes have to adapt to the reef substrate under different conditions (Booth and Beretta 1994; Ebersole 1985; Sale et al.1984; Tolimieri 1998). Depending on specific microhabitat requirements, fishes are able to discriminate, making precise choices about where to settle (Öhman et al. 1998). There is a general agreement that the olfactory system may be developed to guide larval fishes towards the coral reef (Myrberg and Fuiman 2002). Lecchini et al. (2005) demonstrated the use of visual, acoustic/vibratory and olfactory cues by larval schooling pomacentrid *Chromis viridis* for settlement choice. Swimming speeds (Fisher 2005) and audition (Egner and Mann 2005; Leis and Lockett 2005) of late larvae have been recently associated with the ability of damselfish to settle on the reef.

Jones (1991), Williams (1991), and Cheney and Côté (2003) distinguished several individual factors and ecological processes influencing distribution of settlers, post-settlement recruits, juveniles and adult reef fishes. Among these factors and processes were habitat structure (i.e., topographic complexity), resource availability (e.g., space, shelter, food), current flow and water quality, exposure to wave action, presence of settlers, disturbance, intra- and interspecific competition, predation, and facilitation. Habitat structure affects demographic factors such as mortality and growth (Levin et al. 2000). Habitat may have features that qualify as an adequate offer that satisfy species unique requirements, such as settlement site, shelter from predators, food, and

reproduction (Carr and Hixon 1995; Cheney and Côté 2003; Forrester 1990), thus enhancing suitability for occupancy. Higher presence of recruits was positively correlated with dead foliose coral (Lirman 1994), high coral cover (Lirman 1999) and particular coral species (Jones 1988). Forrester (1999) and Öhman et al. (1998) concluded that presence of other settlers as well as resident conspecifics were relevant factors influencing fish distribution. Gutiérrez (1998) observed that the non-random local pattern distribution for adult *Stegastes dorsopunicans* and *S. planifrons* was produced by habitat selection of the recruits. Similar results were obtained by Holbrook et al. (2000) for several species of *Dascyllus* and *S. planifrons*, and by Munday (2002) for four species of *Gobiodon*.

Eggleston et al. (2004) determined the distributions of fishes in six different habitats in Key West National Wildlife Refuge. Pomacentrids presented the highest abundance in offshore reefs, hardbottoms and patch reefs, and the lowest in seagrass, channels and mangroves. Almany (2003), Cleveland and Montgomery (2003), and Robertson (1996) found that *S. planifrons* competitively excluded other damselfish species in the process of territorial defense. The habitat geometry and physical composition may affect individual territory size, and hence population density in certain habitats (Meadows 2001).

Damselfishes are demersal spawners. Female deposits demersal eggs in the nest found within male's territory. Males provide parental care (e.g., defense, ventilation) to the clutch until hatching. Eggs develop for 3-6 days and hatch into yolkless larvae (Wellington and Victor 1989). Damselfish larvae found in

ichthyoplankton surveys were restricted to nearshore waters (Wellington and Victor 1989). Ramírez-Mella and García (2003) found the highest relative abundance of pomacentrid larvae within insular shelf waters, near the shelf edge reef system of La Parguera. Interestingly, Rooker et al. (1997) found *Stegastes* spp. and other reef fish adults in offshore oil platforms within the Flower Garden Banks. After 17-32 days in the water column, *Stegastes* larvae settle, having a size range of 9-14 mm SL (Wellington and Victor 1989; Wellington and Robertson 2001). *Stegastes dorsopunicans* settles at 10.0-12.6 mm SL after 28-30 days of planktonic larval life (Wellington and Robertson 2001). All species show a lunar pattern of settlement with peaks around new moon (Robertson 1992), settling during the evening and transforming overnight (Robertson et al. 1988). Extremely high mortality accounts for immediate daily fish loss after settlement in a rate higher than 10% for a few days, with a posterior sharp decline in mortality (Victor 1986).

Stegastes adustus is an omnivorous territorial species common in the Caribbean reefs and strongly associated with the substrate. Its depth range varies from shallow to moderately deep waters, preferring rubble zones, but regularly inhabiting reef structures. Juveniles are mostly found in sand, rubble and bare rock areas on the back reef and reef crest. This species ingests a wide range of food items, although the most important dietary constituent is benthic algae. Randall (1967) and Emery (1973) report that the diet of *S. fuscus*, (= *S. adustus* in the Caribbean), consists of 51.8-79.2% algae and organic detritus for fish 50-98 mm SL range, and 65.0-92.5% polychaetes, crabs and decapod

shrimp for 20-40 mm SL fishes. Not all adults maintain a territory, but when they

do so, there is an aggressive defense behavior for their epilithic algal mats. This

fish defends individual territory where it cultivates an algal lawn 10-15 mm in

height, which traps sediments to supply its nutritional needs (Potts 1977).

Territories are clearly visible on the reef as distinct patches ("lawns" or "mats") of

relatively dense microalgal growth and are defended from intruding macro-

grazers (e.g. scarids, acanthurids) by resident fishes. Territorial defense consists

of aggression (e.g. attack) against grazers (Foster 1985; Robertson 1984), but

carnivorous predators are ignored. Repelling action reduces grazing pressure

over the algae, which then is able to grow and colonize coral, preventing coral

growth. Wanderer individuals (i.e., females and non-reproductive males) suffer

high predation rate, but are ready to move into vacated higher quality territories.

Early studies on territorial damselfishes were performed in the Florida

Keys by Emery (1973) and in Jamaica by Itzkowitz (1977), previous to the

Acropora and *Diadema* die-off. Given the location of Emery's study, I assumed

that the species he identified as *Stegastes fuscus* Cuvier 1830 is *S. adustus.*

Highest abundance (1.30 fish/m^2) in Florida was found in the breaker area of the

reef, but the tradeoff was that territories were not well defined or defended.

Meanwhile, patch reefs harbored abundances ranging between 0.06-0.28 fish/m^2.

As stated by Shulman (1984) for St. Croix, U.S. Virgin Islands (USVI), an

increase in the number of shelter sites produced an increase in the number of

recruits, explaining the high abundance in the breaker area. There is an

apparent behavioral difference in microhabitat use by different life stages (i.e.,

size classes) of *Stegastes* spp. Microhabitat use explained 32 to 49% of the

variation in abundance among sites for *S. partitus*, *S. planifrons*, and *M.*

chrysurus, and 85 % for *S. adustus* in St. Croix (Tolimieri 1998). Substrate

selection may change at different age related behavior. Ontogenetic patterns of

habitat utilization were shown for *Dascyllus aruanus* (Holbrook et al. 2000) and *S.*

planifrons (Lirman 1994). Itzkowitz (1977) found that approximately 62% of

damselfish were associated with rubble, while 36% were associated with

Acropora spp., and roughly 1% was associated with *Montastraea* spp.

Several types of artificial habitat structures have been used in *Stegastes*

ecological investigations. Evidence shows that *Stegastes* moves to higher quality

territories when these become available. Key determinants for high quality

habitats include territory features that can influence fitness-related parameters

such as growth rates, reproductive success, parasite loads and predation risk.

Small sized reefs built from natural coral material (Jones 1987, 1988), PVC pipes

(Itzkowitz 1990; Itzkowitz et al. 1995), and empty conch shells (Shulman 1984)

have been used to evaluate competition, territoriality, reproductive success

(Itzkowitz and Makie 1986), effects of resource limitation, and recruitment of reef

associated species. Vacant high quality habitats (e.g., nest presence) were

recolonized in shorter time by male *S. diencaeus* in Barbados (Cheney and Côté

2003). Beets (1989) examined the effectiveness of fish attracting devices and

artificial reefs for reef fish assemblages. The combination of these artificial

habitats yielded the highest increase in species richness, abundance, and post

larval recruits. Brock and Norris (1989) obtained the best recruitment results

using concrete cubes to attract commercial and recreational fish species. Chandler et al. (1985) concluded that the greater availability of space allowed support of larger and most diverse fish community.

There are several fish studies for Puerto Rico, mainly in southwest Puerto Rico but no recent damselfish research (Aguilar 2004; Cerveny 2006; Foley 2003; McGehee 1991, 1995). MacDonald (1973) studied the reproductive behavior and social dynamics of *Microspathodon chrysurus*. This fish occupied larger territories than *Stegastes*, with areas between 3.6 and 24.6 m^2. Waldner (1980) conducted a series of studies that demonstrated substrate and depth partitioning at various reefs for eight species of territorial Caribbean damselfishes. Damselfishes preferred *A. palmata* and *A. cervicornis* to *M. annularis* in a coral selection experiment. The study by Waldner (1980) was performed before the *Diadema* and *Acropora* mass mortalities. Hinds (1984) characterized the taxonomic composition of the algal lawns in La Parguera and examined gut contents of *S. planifrons*. Results indicated that *S. planifrons* feed primarily on their algal lawns when compared with natural occurring lawns.

The latest damselfish-specific population study near Puerto Rico was from St. Thomas, USVI (Booth and Beretta 1994). The researchers examined the seasonal recruitment, habitat associations, survival, patterns of distribution and abundance for five of the six *Stegastes* species, not including *S. dorsopunicans* (= *S. adustus*). They found that recruitment occurred largely in summer for four species, meanwhile *S. planifrons* recruited in winter. Miller et al. (2001) reported similar summer recruitment patterns in USVI, except for *S. planifrons*, which

presented a more evenly distributed recruitment throughout the year. Solandt et al. (2003) found that areas of high macroalgal cover influenced size composition, and territorial and breeding behaviors of *S. diencaeus*. Densities were higher in barren areas where macroalgae were not present. Lirman (1999) demonstrated that the highest mean abundance of *S. fuscus* was associated with areas of high relief and areas of high/low coral cover by *A. palmata* in Florida and USVI.

CHAPTER 1

ABUNDANCE, DISTRIBUTION AND SUBSTRATE UTILIZATION

INTRODUCTION

Coral reef fishes are characterized by being strongly associated with reef habitat throughout most of their juvenile and adult life history stages (Choat and Bellwood 1991). The pelagic planktonic larval phase is the only non-reef related stage in their life history cycle (Leis 1991). One factor that can influence juvenile and adult distribution over small spatial scales is the use of microhabitat due to close association of reef fish with the substratum. Factors influencing the use of space resource use by this group of fishes include territoriality, age distribution, and habitat quality (Jones 1991).

The three-spot damselfish *Stegastes planifrons* is a territorial bottom associated fish frequently found in the *Montastraea annularis* species complex (Tolimieri 1995). Almany (2004a) demonstrated that 80% of new settlers in coral species other than *Acropora* were damselfishes. Prior to the *Acropora* decline Itzkowitz (1977) found that adult *S. planifrons*, *S. adustus* and *S. leucostictus* were found in higher abundance on staghorn and elkhorn coral than on other substrates, while less than 1% was associated with *Montastraea* spp. Pomacentrids had the highest abundance in offshore reefs, hardbottoms and patch reefs, and the lowest in seagrass, channels and mangroves (Eggleston et al. 2004).

Stegastes adustus, Caribbean dusky damselfish, is a territorial fish that strongly associates with the substrate. This fish prefers rubble zones of the

shallow and moderately deep waters but regularly inhabits the reef structure.

Juveniles are mostly found in sand, rubble and bare rock areas on the back reef

and reef crest. Benthic algae are the most important constituent in its

omnivorous diet (Emery 1973; Hinds 1984; Potts 1977; Randall 1967) which

they cultivate within their territories and aggressively defend against other

herbivores (e.g., scarids, acanthurids) including congeners, while ignoring

predators (Almany 2003; Cleveland and Montgomery 2003; Foster 1985;

Robertson 1984, 1996). A distinctive "lawn" or "mat" is present in territories

maintained by adults even though not all adults keep one. Repelling action

reduces grazing pressure over the algae, which then is able to grow and colonize

coral, preventing coral growth. Individuals with none or low quality territory are

prone to predation but move into higher quality territories shortly after these

become unoccupied.

Emery (1973) estimated densities of 1.30 fish/m^2 for *S. fuscus* (=*adustus*)

in the breaker area on either poorly delineated or defended territories. Lower

abundances were in the range of 0.06-0.28 fish/m^2 for other locations. Shulman

(1984) explained the high abundance of recruits in the breaker area of USVI as a

direct relationship with the number of shelter sites. There is an apparent

ontogenetic pattern in microhabitat use by *S. planifrons* (Lirman 1994) and

Dascyllus aruanus (Holbrook et al. 2000). Tolimieri (1998) found that

microhabitat use explained 32 to 49% of the variation in abundance among sites

for *S. partitus*, *S. planifrons*, and *M. chrysurus*, and 85 % for *S. adustus* in St.

Croix.

In this study I evaluated the spatial and temporal variations in the population of the Caribbean dusky damselfish *S. adustus* in La Parguera, southwestern Puerto Rico. I studied how benthic microhabitat resources were utilized by this fish an looked for correlated patterns of development. To accomplish these objectives I hypothesized that abundance was significantly different among reefs or months along a year, and that there were significant relationships between abundance and substrate composition, particular coral species or rugosity.

MATERIALS AND METHODS

Fish Abundance Surveys

Five reefs were selected within La Parguera Natural Reserve reef system in southwestern Puerto Rico for this study (Fig. 1). The sites were San Cristóbal (67º 04.604' N, 17º 56.438' W), Mario (67º 03.379' N, 17º 57.106' W), Laurel (67º 03.486' N, 17º 56.440' W), Media Luna (67º 02.931' N, 17º 56.093') and Turrumote (67º 01.085' N, 17º 56.084' W). These are emergent fringing reefs with the typical reef profile: back reef, reef crest, fore reef, reef slope and reef base (Goreau 1959).

Fish were surveyed monthly using SCUBA from August 2005 to July 2006. Abundance surveys were performed during early morning between the first quarter and the full moon of the month to increase the chance of observing recruits since most settlement for damselfishes and other reef fishes occurs around the new moon (Caselle and Warner 1996; Robertson 1992). This schedule minimized the potential of not observing recruits due to post-settlement

processes (competition, mortality (disease/predation), relocation (i.e., movement) (Jones 1991).

Five replicate permanent linear belt transects were established roughly parallel to the reef crest along the fore reef of each site after a preliminary survey to determine the necessary number of replicates. Water depths were less than seven meters in all areas sampled, ranging from 1.9 m in Mario to 6.9 m in Media Luna. Mean abundance was estimated as the total number of fish within each 10 m long x 2 m wide transects (i.e., 20 m^2). This transect dimension was intended to increase the accuracy and precision of fish counts, especially on recruits, allowing survey of the entire fish size range (Doherty 1991). Small spatial scale is most appropriate when trying to find evidence for a pattern of habitat choice when there is a variety of different substrates (Munday 2002; Tolimieri 1995).

A measuring tape was extended between rebars driven into the reef marking the beginning and end of transect center line. Fish were counted 2-3 minutes after extending the measure tape. I actively searched for cryptic recruits. To minimize edge effect, if a damselfish was not within transect, but at least 50% of its territory was within transect, then it was recorded as within. The size of each fish was estimated and recorded as standard length (SL) to the nearest centimeter (cm).

Characterization of the Study Area and the Territories

To relate variation in the abundance of *S. adustus* to composition of the substrate, each transect was quantified using the point-intercept technique (Loya

1978). The type of substratum directly beneath the measure tape was recorded every 25 cm. The categories used for substrate composition of the territory were dead coral, sand, colonized pavement, rubble, live hard coral, gorgonian, sponge, zoanthid and calcareous algae. Live coral was identified to species level. Composition data was expressed as percentage.

Substrate rugosity index was determined using the chain link method and defined as the ratio of the total length of the chain loosely but carefully draped to the contour of the substratum along the centerline of the transect to the linear length of the transect (10m). The higher the index the more complex the substrate was, being index equal to 1.0 a flat substrate. Areas of higher structural complexity may offer more protection to fish, thus represent a potential direct positive correlate for fish abundance.

All territories found within transects were once quantified for the same categories of substrate cover composition by using a 1-m^2 quadrat to record the percentage cover of each category. The location of territories was determined by observing the limits in the movement of damselfish for 3-5 minutes and distinguishing the algal lawn. Algal lawn was defined as the substrate covered by a distinctive turf of short filamentous algae (<1cm high) that was vigorously protected by the damselfish.

Statistical Analysis

Data was tested for normality and homoscedasticity for applicability of parametric analyses (Sokal and Rolf 1981); non-parametric statistical analyses

were applied when parametric assumptions were not met. Differences in spatial

and temporal patterns of abundances of fishes were compared using ANOVA.

Distribution patterns within each reef were determined using the index of

dispersion, variance-to-mean ratio (Sokal and Rolf 1981).

Correlations and regressions were used to examine relationships

between: 1) mean fish abundance and the number of fish with territories, 2) %

cover of microhabitats on each transect and % cover of microhabitat within

territories of each transect, 3) effect of substrates on mean damselfish

abundance, 4) effect of % cover of microhabitats within the territories on the

number of fish with territories, and 5) effect of substrate rugosity on mean

abundance.

RESULTS

A total of 3,437 fish were observed in all five reefs during the twelve month

study. The mean abundance of *Stegastes adustus* in 20m^2 belt transects was

11.5 ± 0.4 ind/20m^2 (x̄ ± SE; n = 300 counts; range = 1-30 fish/transect). The

study mean abundance of *S. adustus* showed moderate variation and was

significantly different between reefs at the studied depths in La Parguera

(Repeated Measures 2-way ANOVA, p<0.05; Fig. 2). Abundance ranged

between 15.9 ± 0.8 ind/20m^2 at Mario reef and 7.9 ± 0.4 ind/20m^2 at Media Luna

reef. San Cristobal reef hosted 12.5 ± 0.6 ind/20m^2, while Laurel and Turrumote

reefs showed 11.7 ± 0.6 ind/20m^2 and 9.4 ± 0.3 ind/20m^2 respectively.

Monthly mean abundance data of *S. adustus* at the reef stations sampled

is presented in Table 1. Statistically significant interaction effects between sampling sites and dates were found for the abundance of *S. adustus* (Repeated Measures 2-way ANOVA, p<0.05; Fig. 3). This is indicative that differences of abundance between sites depend on dates and vice versa. There was not any consistent pattern of *S. adustus* abundance throughout the study at the various sites observed, except for significant monthly differences of abundance at Mario (20.0 ± 3.4 ind/20m^2) and San Cristobal (18.4 ± 2.6 ind/20m^2) reefs, in which the main temporal pattern was a peak in abundance in May at both reefs. Abundance declined again in June at San Cristobal, whereas it remained relatively high until July at Mario.

The study mean relative abundance of juveniles varied between 26.7% (196 out of 735 total fish) at San Cristobal reef and 40.4 % (281 out of 696 total fish) at Laurel reef (Fig. 4). There were significant differences (p<0.001) in the second order interaction of the mean abundances of stages-reefs-months, thus Repeated Measures 2-way ANOVA were used to evaluate separately each stage for simplicity and meaningful interpretation. Reefs and months had a significant interaction within juveniles (p<0.001) and adults (p<0.05; Fig. 5). Juvenile *S. adustus* (3-5 cm) were present at all reef stations surveyed and on all sampling dates (Table 2), except at Medial Luna reef during September (Fig. 5). In this stage, only September resulted with significant differences (Tukey test, p<0.05) among reefs. Differences within reefs resulted for Turrumote (Tukey test, p<0.05). Largest difference along the year was recorded in Mario (p<0.001). Highest mean abundance was observed at Laurel in March (8.6 ± 2.3 ind/20m^2),

while the lowest was zero at Media Luna in September. For adults, abundance

between reefs differed significantly in August and July (Tukey test, p<0.05).

Significant differences in abundance between months were observed in Media

Luna and Turrumote reefs (Tukey test, p<0.05). Mean abundance was highest in

June on Mario (13.6 ± 2.9 ind/20m^2) and lowest during March in Media Luna (2.6

± 0.8 ind/20m^2).

Abundance of recruits (<2 cm SL) at all reefs studied was very low (n=72).

Recruits were scarce in Turrumote (n=5) and not observed at all in Media Luna.

There were few fish in Laurel (n=6) and San Cristobal (n=14). Meanwhile, Mario

hosted the most recruits (n=47). A prominent recruitment period was observed at

Mario with a maximum of 12 recruits in July and seven in June. Another high

period of recruitment was observed in October and November with nine and

seven recruits respectively (Fig. 6). Statistical analysis was not attempted due to

limited sample size.

There were 88 territories established by *S. adustus* in all reefs combined,

from which 96.6% were adult fish and 3.4% were juveniles. The mean number of

territories per reef was not significantly different between sites (1-way ANOVA,

p>0.05). The mean number of territories varied between a maximum of 4.8 ± 1.0

territories/20m^2 at San Cristobal and a minimum of 1.6 ± 0.2 territories/20m^2 at

Mario (Fig. 7). Variation was relatively low (CV = 30.6%- 50.8%), except at

Media Luna (e.g., 61.4%).

The correlation between mean fish abundance and total number of

territories per reef was slightly positive (slope=0.07), but weak and not significant

(r=0.15, p>0.05). This suggests that the number of territories is not influenced by the amount of fish present on the reef, but rather by adequate habitat availability and possibly depth. Fish may recruit in shallow waters near the reef crest where refuges are available and later migrate to deeper water where more variety of substrate types are available.

All substrate types were recorded in transects and territories, except for sand in Laurel (Table 3). Colonized pavement contributed the highest percentage cover in both transects (31.5%) and territories (40.0%). Substrate cover by dead coral was observed in higher proportion at the territories (17.8%) than in transects (11.9%) while the opposite occurred with live coral, which covered more in transects (19.0%) than in territories (10.4%). Overall, a significant positive correlation resulted from the percent cover in substrate composition between territories and transects (r^2=0.52, p<0.05).

Microhabitat features revealed high variability (>50%) at all sites except in colonized pavement category, making more difficult the detection of patterns in substrate use. All reefs had a significant higher cover by colonized pavement (2-way ANOVA, p<0.05; Fig. 9). Additional significant differences in lesser covering substrate types of dead and live coral resulted in their comparison within the transect-territory location and between other substrate types at the reefs studied. Individual relationships between percent cover by substrate category in territories and transects were not significantly correlated (p>0.05; Table 4). Mean percent cover by dead coral, colonized pavement and live coral were not different between reefs (2-way ANOVA, p>0.05; Figure 10). This may

be indicative that *S. adustus* has no choice when selecting a degraded habitat given the actual state of the coral reefs in La Parguera, but is also able to modify its territory to satisfy its living necessities.

Montastraea annularis was significantly the dominant scleractinian coral overall (2-way ANOVA, Tukey test, p<0.001) representing 8.7% and 4.9% in transects and territories respectively in terms of % substrate cover (Table 5; Fig. 11). *Porites astreoides*, *P. porites*, *Millepora* spp., *Agaricia* spp., *M. cavernosa*, *Siderastrea siderea*, *Diploria* spp. and a few other coral species were present in lower % substrate cover. Substrate cover by *M. annularis* on transects was highest in Media Luna (12.2%) and lowest in Laurel (3.9%), while on territories it was highest in Mario (11.5%) and lowest in Laurel (2.5%) (Fig. 12). Such variations were not significantly different between the reefs studied (2-way ANOVA, p>0.05).

Rugosity indices varied from 1.29 ± 0.05 at Media Luna to 1.44 ± 0.02 at Mario. There was no significant difference in rugosity between reefs (1-way ANOVA, p>0.05). Relief was relatively uniform among reefs, lowest variability was observed in Mario (CV=3.4%) and highest in Turrumote (CV= 9.3%) (Fig. 13).

In general, abundance by *S. adustus* varied independently from the predominant reef substrate cover types, such as live coral, sand, rubble and dead coral. Positive and negative correlations resulted between mean fish abundance and percent substrate cover. A significant positive correlation was observed between mean fish abundance and the percent cover by calcareous

algae (e.g., *Halimeda opuntia*) (r=0.49, p<0.05), whereas significant negative

correlations resulted versus substrate cover by gorgonians (*Gorgonia* spp.,

Plexaura spp.) (r=-0.43, p<0.05) and zoanthids (e.g., *Palythoa caribaeorum*)

(r=-0.40, p<0.05; Table 6). Relationships with all other substrate types, including

M. annularis, were not significant.

Mean fish abundance was positively correlated with substrate rugosity, but

the relationship was not statistically significant (p>0.05) for any of the fish groups.

The effect of rugosity was more evident on all fish (r=0.32) than on juvenile

(r=0.20) and adult fish (r=0.29; Table 7), suggesting that rugosity might play dual

functionality depending on the fish stage. For juveniles, rugosity offers refuge

from predators, allowing for higher probabilities of reaching reproductive size. To

adults it may be beneficial in terms of providing a higher quality territory in which

to mate and reproduce.

The total number of territories of *S. adustus* was positively correlated only

to dead coral cover within its territory (r=0.42, p<0.05; Table 8). Correlations

with other substrate types were low and not significant (p>0.05).

DISCUSSION

The mean abundance of *Stegastes adustus* in this study was similar to

that reported recently by other authors in La Parguera (Aguilar-Perera 2004;

Foley 2003; McGehee 1991, 1994), Florida (Lirman 1999), USVI (Lirman 1999;

Tolimieri 1998) and Panamá (Gutiérrez 1998). Earlier pomacentrid studies in La

Parguera (Waldner 1980; Waldner and Robertson 1980) showed lower

abundance values. Studies within a marine protected area in Florida reported similar abundance values (Wallman et al. 2004) or higher (Wilkes et al. 2008) to this study, but in the latter the fish were mainly adults associated with *A. cervicornis*. Non-random distribution patterns were observed for pomacentrids *Dascyllus* spp. (Holbrook et al. 2000) and gobiids (Munday 2002). Gutiérrez (1998) observed that the non-random local pattern of distribution for *S. adustus* and *S. planifrons* was produced by habitat selection of the recruits, whereas Tolimieri (1998) documented a non-random pattern for *S. adustus* in the back reef and random in the fore reef. Distribution patterns of adult coral reef fishes are generally governed by those of recruits, which are most of the time related to substrate associations.

The temporal increase of mean abundance in Mario and San Cristobal reefs and in total recruit abundance in Mario was near to those reported for other *Stegastes* species in terms of quantity and/or timeframe, suggesting a seasonal pattern for *S. adustus* in some populations within La Parguera. Recruitment data from USVI (Booth and Beretta 1994) indicated strong seasonality at both studied sites that was independent of depth. The latter statement contrasts with the results of my study in which shallower Mario reef showed higher recruitment, in terms of number of recruits and season, in summer and another peak in fall. While Waldner (1980) and Waldner and Robertson (1980) reported a peak in August. McGehee (1995) showed settling pulses for four *Stegastes* species during September-October in La Parguera. Seasonality matched that of other coral reef fish families in USVI (Caselle and Warner 1996; Miller et al. 2001).

Only one of the reviewed *Stegastes* studies (Holbrook et al. 2000) correlated the density of adults to the density of its recruits. Abundance and distribution may be driven by biological variation in spawning and associated processes in survival of larvae, settlers and recruitment pulses. A factor driving the observed distribution of abundance may be the patterns of reef fish egg and larval dispersion in southern Puerto Rico (Appeldoorn et al. 1994; Hensley et al. 1994; Ramírez-Mella and García 2003). *Stegastes* larvae spend almost one month in the water column before settling, then either currents carry larvae away of the natal reef system or local biophysical and behavioral processes act on larvae retention, hence producing self-recruitment (Cowen et al. 2000; Lecchini et al. 2005; Leis et al. 1996; Leis and Lockett 2005; Paris and Cowen 2004; Robertson et al. 1993; Swearer et al. 2002). Some fish species settle and recruit throughout the year and may not show a seasonal increase, while others produce larvae at a specific time showing a strong peak after a spawning aggregation (Esteves-Amador 2005). Environmental factors and ecological processes during settlement (e.g., habitat availability and selection, density of conspecifics), post-settlement (e.g. mortality), recruitment (e.g. growth) and post-recruitment (e.g., predation, competition, dispersal/migration) also affect abundance and distribution patterns of coral reef fishes. Temporal differences in total abundance of recruits in this study may be due to a shift in recruitment towards the summer due to a possible variation of oceanographic factors. Some of these factors may be high temperature stress (Booth and Beretta 2002; Pratchett et al. 2006), local currents (Esteves-Amador 2005; Ojeda-Serrano

2002) or wave action between seasons and sites (Booth and Beretta 1994; McGehee 1994). Sea surface temperature in La Parguera exceeded the 29.5°C coral temperature threshold between late April and mid November, when maximum sustained temperature exceeded 31.0°C and reached 32.0°C in some instances (NOAA 2005). Booth and Beretta (1994) observed overall recruitment of *Stegastes* species in the USVI in 1991-1992 during those months. It is possible that the reproductive cycle was sparked in that period affecting recruitment variability within that time range. McGehee (1994) suggested that the synergistic effect of water movement energy, depth and substrate size affects the abundance and distribution of aquatic organisms other than fishes. High variability of recruitment pulses was observed by Miller et al. (2001) among and within a continuous 31 month period (1997-1999) in USVI for several families of coral reef fishes. Tolimieri (1995) reported similar results for *S. planifrons* in the summers of 1991-1993 in USVI and Virgin Gorda. Variability within and between years and among sites was evident for *Thalassoma bifasciatum* (Caselle and Warner 1996). Another plausible justification may be the combination of higher recruitment pulses and good reef health in years past when the substrate was in better state for damselfish biological and ecological necessities. The number of recruits observed in this study may lead to lower abundance of *S. adustus* in La Parguera or elsewhere, but a larger scale multiannual survey is needed to corroborate if this was the typical recruitment and juvenile-adult abundance pattern.

Minor scale local effects (e.g., disturbance, food availability, currents) and variability induced by the sampling spatial scale cannot be discarded. Proposed explanations need to be studied in a longer timeframe coupled with environmental measurements.

The spatial and temporal differences in distribution observed between and within juveniles and adults in this study, as well as that observed qualitatively from recruits may be explained by ecological processes like ontogenetic shift, habitat associations and presence of established residents (i.e., priority effect) allowing coexistence. Limitations of available data in the literature constrain comparison of spatial and seasonal data for juveniles and adults from this study. No other study has reported a year long survey except for Waldner (1980) and Waldner and Robertson (1980), but their data shows some inconsistence. Small scale ontogenetic variation was observed in La Parguera (Aguilar-Perera 2004) and elsewhere (Booth and Beretta 1994; Gutiérrez 1998; Lirman 1994; Holbrook et al. 2000), where fish migrated either from shallow to deep zones or between substrates (e.g., from live to coral rubble and vice versa) at same depth within the reef. Booth and Beretta (1994) reported that small juveniles of all *Stegastes* species, except *S. adustus*, associate with live coral but that adults associate with dead coral rubble. But Wilkes et al. (2008) in Dry Tortugas National Park showed that density of juveniles was greater in rubble, while that of adults was higher in live *A. cervicornis*. Shulman (1984) found that juvenile *S. leucostictus* prefer to live within *Porites porites* corals. Similarly, fish movement was noticed in larger scale by Aguilar-Perera (2004) and Pratchett et al. (2008),

and a marked ontogenetic pattern of substrate utilization was observed by the latter.

Cohabitation by conspecifics (Booth and Beretta 1994), congeners (Robertson 1984, 1996), even predators (Almany 2003, 2004b) may or may not interfere or facilitate the arrival of new fish joining the population by either recruitment, or relocation (Cheney and Côté 2003). Priority effect tended to reduce abundance of recruits (Almany 2004a, c; Carr and Hixon 1995), but not of adults (Almany 2004a, c). Coral reef fish can be regulated by density dependence, interaction modifications, and resource partitioning. Neither resource nor interference competition was observed in La Parguera (Waldner 1980), USVI (Booth and Beretta 1994), Panamá (Waldner and Robertson 1980) and Australia (Doherty 1983) because of stage segregation and resource partitioning by the dietary requirements of recruit, juvenile and adult fishes.

Even though no significant differences were observed in the number of territories per site, it is clear that Mario reef showed the lowest amount, in contrast to the observed highest abundance there, in agreement with Emery (1973). An increase in the number of shelter sites results in a rise of the number of reef fish recruits in the breaking zone (Shulman 1984). Qualitatively, Mario had the highest amount of refuge holes, allowing higher number of recruits, but with fewer territories. The presence of only three juvenile *S. adustus* in Turrumote keeping a territory is consistent with the reported biology and behavior of the species in which the main purposes for adults to maintain and defend a territory are reproduction and feeding (Foster 1985; Itzkowitz 1990; Robertson

1996; Solandt et al. 2003) while juveniles are busy near a hole seeking immediate refuge if threatened, thus ensuring survival and growth (Hixon and Beets 1993; Shulman 1984). Fish may migrate from shallow to deeper zones or hide in deeper sites until attaining larger sizes and are able to occupy and defend suitable spaces (Cheney and Côté 2003; Holbrook et al. 2000; Shulman 1984; Tolimieri 1995).

The observed variability of mean abundance and substrate categories in transects prevented detection of clear patterns in microhabitat associations that explained substrate utilization in this study. Apparently there is no pattern of substrate category or coral species which determines the abundance of *S. adustus* in La Parguera. Field observations indicate that *S. adustus* may be an "opportunistic generalist" species. McGehee (1995) sustained that *S. variabilis* had the ability to thrive in a variety of locations given that it did not exhibit any particular specialization or a need for a specific habitat. Pratchett et al. (2008) determined that some species of *Chaetodon* are less specialized than others, thus distributed across a broad range of habitats.

The presence of calcareous algae, even in low reef substrate cover, seemed to be important for *S. adustus*. The positive relationship of mean abundance to calcareous algae may be due to the additional structure provided in barren substrate by its growth form and the additional surface area for overgrowing algal turf hence benefiting territorial *Stegastes* species by promoting activity and higher abundance (Solandt et al. 2003; Tolimieri 1995). *Palythoa caribaeorum* is a fast-growing secondary colonizer of disturbed areas (e.g.,

degraded coral reefs), and they secrete powerful palytoxin, thus outcompete other organisms by rapidly acquiring space and to protect themselves (see references in Acevedo-Soto 2007). The zoanthid was mainly observed along transects, but rarely within territories, and its competitive effects may be the reason for the negative association with mean fish abundance. Gorgonians apparently to do not provide any evident benefit to *S. adustus* in terms of structure and food thus avoiding areas colonized by this coral group. Lugo (2004) suggested that areas covered by gorgonians may be less attractive to long-spine urchins because of the little protection available due to a low number of crevices.

Even though colonized pavement was the most abundant substrate type, there was no relationship between mean fish abundance and pavement cover that could explain the variation in abundance and difference in spatial distribution. Newly settled *Thalassoma bifasciatum* were most common on pavement (Caselle and Warner 1996). Higher abundance and persistence of *Acanthurus bahianus* settlers was related to pavement association in the back reef, probably due to high quality food resources reducing the need for emigration (Risk 1997). Although pavement is much less complex in structure than some other substrata, it contains holes and crevices that were used and aggressively defended for shelter. The persistence in pavement, due to refuge and food, was related to the increase in total length of surgeonfish and determined patterns of juvenile distribution. Strong site fidelity and high

survivorship of *S. planifrons* recruits was observed in La Parguera hence a long life expectancy (McGehee 1995).

Assuming that dead coral within the territories is a transition category between live coral and pavement, the positive relationship between this substrate type and the total number of territories per transect in this study suggests some alternative explanations. *Stegastes adustus* may acquire a territory with algal turf by moving either into an area with either already dead coral or to a locality with live coral and then killing the coral by nipping. These two substrates eventually turn into pavement. Live coral was observed more frequent in transects than in territories while pavement was significantly higher in territories. Dead coral varied in its cover and in conjunction with pavement cover may be a sign of reef health not related to activities of *S. adustus.*

Data from this study appears not to be related to the intense bleaching event of 2005 in the Caribbean, apparently its effect was not instantaneous over populations of *S. adustus* in La Parguera because of the observed not different abundances within three reefs in the study period. Bleaching was related to lower recruitment, change in diversity and assemblage, decrease in abundance of adults (Booth and Beretta 2002), and to temporal variation in the abundance of *Chaetodon* species after a decline of coral cover due to an event in the Pacific (Pratchett et al. 2006). Overfishing caused the alteration in the dynamics of damselfishes due to a shift to algal dominated reefs associated with removal of predators and large herbivores (Ceccarelli et al. 2006; Solandt et al. 2003).

Bleaching and successive algal colonization could be disastrous for the coral reef.

This study demonstrated that differences and similarities with results of other studies in the Caribbean and Western Atlantic validate the inherent variability of coral reef fish abundance on a wider spatial scale. Variability in the structure of juvenile and adult coral reef fish population is usually linked to stochastic spatio-temporal variation in larval supply and recruitment (Jones 1990; Sale and Douglas 1984). Some differences in microhabitat use were not explained. It might be that sites were chosen by juveniles and adults not due to preferential selection but utilized by opportunism and a weak need for specific habitat use. Ultimately, being this coral reef fish specie not as specialized as previously thought. The relationship between microhabitat use and abundance might have been weakened or disrupted by ontogenetic changes as suggested by Gutiérrez (1998), Lirman (1994) and Tolimieri (1998). To elucidate recruitment patterns influencing juvenile and adult distribution, long term studies that examine the recruitment density of *S. adustus* and its relation to adult, density at both wider local and regional scales are necessary. Supplementary manipulative experimentation at wider spatial and temporal scales may be essential to identify those patterns. Minor local scale effects or factors not examined in this study may be hindering identification of patterns. This approach will follow the well established perspective that views marine populations as metapopulations (Sale et al. 2006).

Table 1. Monthly mean abundance (x̄ ± SE) of *S. adustus* at the five reefs studied in La Parguera. n=5 transects per reef per month.

Month	Reefs				
	San Cristobal	Mario	Laurel	Media Luna	Turrumote
August	14.2 ± 2.1	13.2 ± 2.0	12.2 ± 3.0	9.0 ± 1.6	9.0 ± 1.1
September	13.6 ± 0.7	12.2 ± 1.5	12.0 ± 2.6	7.2 ± 1.6	8.8 ± 1.0
October	11.0 ± 0.9	15.8 ± 2.5	9.8 ± 1.9	10.2 ± 1.5	8.2 ± 1.3
November	13.4 ± 1.6	15.6 ± 3.1	12.4 ± 2.8	7.8 ± 1.0	8.6 ± 1.0
December	12.8 ± 1.3	17.8 ± 3.6	12.2 ± 3.1	7.6 ± 0.9	10.0 ± 1.5
January	11.4 ± 2.3	13.8 ± 2.6	13.0 ± 2.2	8.4 ± 1.1	9.4 ± 1.4
February	11.8 ± 2.5	13.8 ± 3.2	11.2 ± 2.4	7.6 ± 1.3	8.6 ± 0.9
March	10.2 ± 2.6	11.0 ± 2.7	13.6 ± 2.5	7.0 ± 2.2	8.4 ± 0.7
April	11.6 ± 2.1	18.2 ± 2.1	10.2 ± 1.5	7.6 ± 1.5	11.4 ± 1.2
May	18.4 ± 2.6	20.0 ± 3.4	13.4 ± 1.8	8.2 ± 1.8	10.0 ± 1.3
June	12.8 ± 2.5	19.4 ± 3.9	10.0 ± 1.6	7.6 ± 1.6	10.4 ± 1.5
July	8.6 ± 1.9	19.4 ± 3.2	10.4 ± 1.3	6.0 ± 0.9	10.0 ± 0.9

Table 2. Monthly mean abundance (x̄ ± SE) by stages of *Stegastes adustus* in reefs of La Parguera. Mean of 25 transects at 1.0-6.7 m depth on San Cristobal, Mario, Laurel, Media Luna and Turrumote reef sites.

Month	Life Stage		
	All	Juveniles	Adults
August	11.5 ± 1.1	3.7 ± 0.6	7.8 ± 1.6
September	10.8 ± 1.2	2.4 ± 0.9	8.3 ± 0.6
October	11.0 ± 1.3	2.2 ± 0.7	8.4 ± 0.8
November	11.6 ± 1.5	2.3 ± 0.4	9.0 ± 1.0
December	12.1 ± 1.7	4.6 ± 1.0	7.3 ± 1.0
January	11.2 ± 1.0	3.4 ± 0.3	7.6 ± 1.1
February	10.6 ± 1.1	4.4 ± 0.8	6.0 ± 0.6
March	10.0 ± 1.1	4.8 ± 1.0	4.8 ± 0.9
April	11.8 ± 1.8	3.2 ± 1.0	8.6 ± 0.9
May	14.0 ± 2.3	5.2 ± 1.0	8.5 ± 1.3
June	12.0 ± 2.0	3.0 ± 0.6	8.9 ± 1.2
July	10.9 ± 2.3	4.8 ± 1.0	5.6 ± 1.0

Table 3. Mean reef substrate cover (%) by substrate categories on San Cristobal, Mario, Laurel, Media Luna and Turrumote reefs in La Parguera. Data is for five replicate transects per reef (n=25) and for territories (n=88) occupied by *Stegastes adustus*.

Substrate type	% Cover	
	transect	territory
Dead coral	11.9	17.8
Sand	0.6	4.9
Colonized pavement	31.5	40.0
Rubble	14.0	8.9
Live coral	19.0	10.4
Gorgonian	4.8	2.3
Sea grass	2.3	4.6
Zoanthid	7.6	5.0
Calcareous algae	8.2	6.0

Table 4. Relationship (Pearson's r-values) between the mean % cover of nine substrate categories in transects and territories. SC-San Cristóbal, M-Mario, L-Laurel, ML-Media Luna, T-Turrumote. dc-dead coral, sa-sand, pa-colonized pavement, ru-rubble, lc-live coral, go-gorgonian, sg-sea grass, zo-zoanthid, ca-calcareous algae. Dashes (-) indicate that there was no substrate cover in that category. n= 0-7 territories per transect. Significance of correlations were calculated for all reefs combined (n=25) but not for each reef due to small sample size (n=5). *p<0.05, otherwise not significant.

Reef	Substrate Categories								
	dc	sa	pa	ru	lc	go	sg	zo	ca
SC	0.08	-	0.30	0.40	0.31	-0.45	-0.48	0.72	-0.35
M	0.82	0.81	-0.15	-0.78	-0.18	-	-	-	0.06
L	-	-	-0.20	-0.83	0.08	0.23	0.86	0.77	0.98
ML	0.90	-	0.54	-0.64	0.42	-0.74	0.59	0.04	-
T	-0.40	-	-0.50	-0.64	0.32	-0.17	-	0.75	0.87
all	0.17	0.38	0.13	-0.12	0.10	-0.01	0.75	0.42*	0.59

Table 5. Mean % reef substrate cover values for the observed coral species on San Cristobal, Mario, Laurel, Media Luna and Turrumote reefs in La Parguera. Data is for five replicate transects per reef and for territories (n=88) occupied by *Stegastes adustus*.

Coral species	% Cover	
	transect	territory
Porites astreoides	2.1	1.3
P. porites	2.0	0.8
Millepora spp.	1.8	1.1
Agaricia spp	0.5	0.0
Montastraea annularis	8.7	4.9
M. cavernosa	1.2	0.6
Siderastrea siderea	0.6	0.8
Diploria spp.	1.2	0.2
others	0.3	0.2

Table 6. Relationship (Pearson's r-values) between the mean % cover of nine substrate categories in transects and mean fish abundance. SC-San Cristóbal, M-Mario, L-Laurel, ML-Media Luna, T-Turrumote. dc-dead coral, sa-sand, pa-colonized pavement, ru-rubble, lc-live coral, go-gorgonian, sg-sea grass, zo-zoanthid, ca-calcareous algae. Dashes (-) indicate that there was no substrate cover in that category. Significance of correlations were calculated for all reefs combined (n=25) but not for each reef due to small sample size (n=5). *p<0.05, otherwise not significant.

Reef	Substrate Categories								
	dc	sa	pa	ru	lc	go	sg	zo	ca
SC	0.14	-	0.85	-0.12	-0.33	0.88	-0.62	-0.59	0.22
M	0.20	-0.52	0.38	0.28	-0.84	-	-	0.48	-0.04
L	-	-	0.70	-0.31	-0.33	-0.95	0.41	-0.01	0.33
ML	0.26	-	0.40	0.58	-0.57	-0.67	0.36	0.15	-
T	0.73	-0.95	-0.23	0.23	-0.82	-0.41	-	-0.34	0.61
all	0.12	0.16	0.05	0.13	-0.36	-0.43*	0.07	-0.40*	0.49*

Table 7. Relationship (Pearson's r-values) between mean abundance and rugosity. SC-San Cristóbal, M-Mario, L-Laurel, ML-Media Luna, T-Turrumote. Significance of correlations were calculated for all reefs combined (n=25) but not for each reef due to small sample size (n=5). No significant relationships were observed.

Reef	Life Stage		
	All	Juveniles	Adults
SC	0.07	0.15	-0.11
M	-0.03	0.56	-0.31
L	-0.23	-0.58	0.17
ML	0.84	0.77	0.45
T	-0.04	-0.28	0.40
all	0.32	0.20	0.29

Table 8. Relationship (Pearson's r-values) between the mean % cover of nine substrate categories in territories and total number of fish with territories. SC-San Cristóbal, M-Mario, L-Laurel, ML-Media Luna, T-Turrumote. dc-dead coral, sa-sand, pa-colonized pavement, ru-rubble, lc-live coral, go-gorgonian, sg-sea grass, zo-zoanthid, ca-calcareous algae. Dashes (-) indicate that there was no substrate cover in that category. Number of territories per transect = 0-7. Significance of correlations were calculated for all reefs combined (n=25) but not for each reef due to small sample size (n=5). *p<0.05, otherwise not significant.

Reef	Substrate Categories								
	dc	sa	pa	ru	lc	go	sg	zo	ca
SC	0.79	-0.10	-0.17	-0.12	0.46	-0.70	0.98	-0.93	-0.45
M	0.41	-0.82	-0.65	-0.10	0.38	-	-0.31	0.41	-0.72
L	0.84	-	-0.11	-0.13	0.68	0.86	0.60	-0.25	-0.69
ML	0.64	0.35	0.77	0.40	0.39	0.78	0.83	0.92	0.35
T	0.23	-	0.20	0.10	-0.92	0.66	-0.06	0.26	0.04
all	0.42*	-0.06	0.13	0.12	-0.12	0.21	0.37	-0.06	-0.31
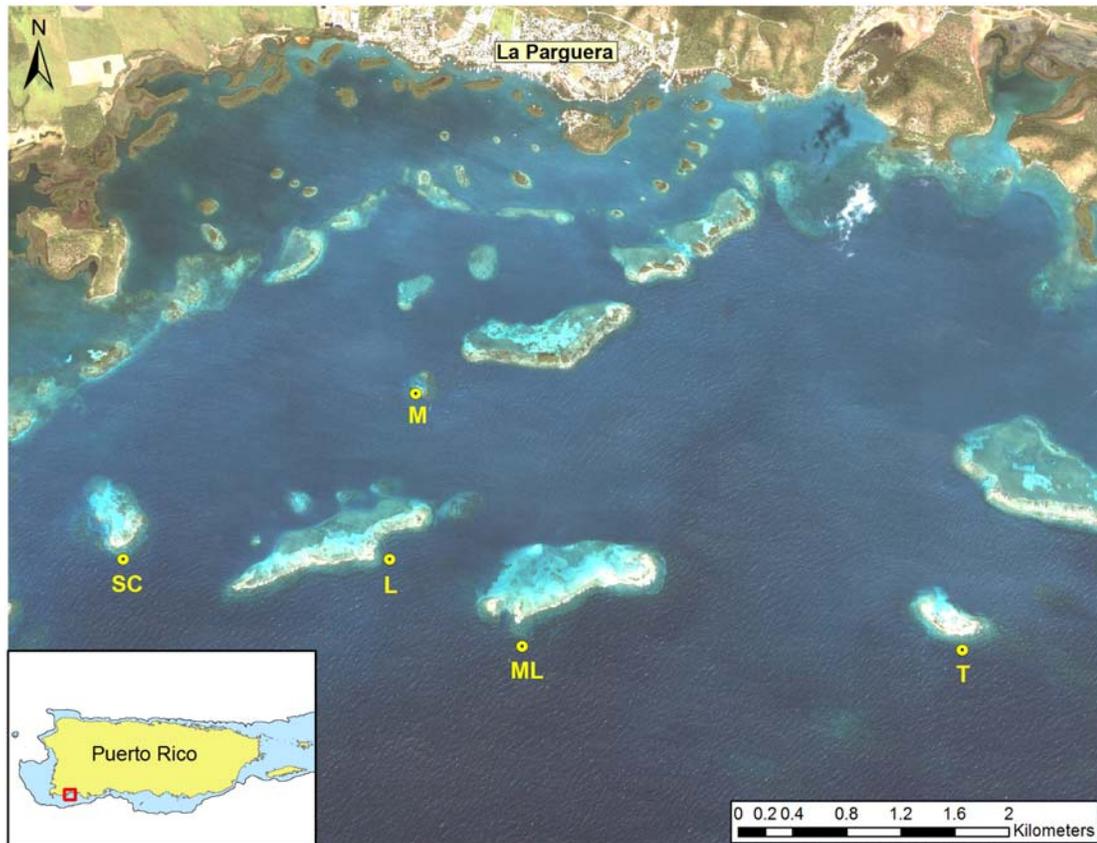
Figure 1. Location of the five sampling sites within La Parguera Natural Reserve reef system in southwestern Puerto Rico. SC-San Cristóbal, M-Mario, L-Laurel, ML-Media Luna, T-Turrumote.
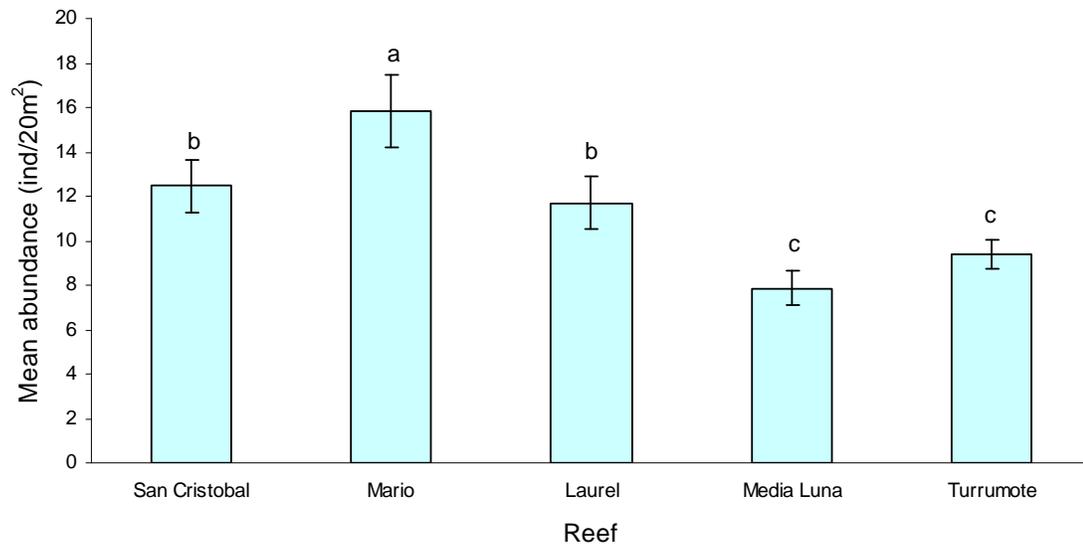
Figure 2. Study mean abundance of *Stegastes adustus* as determined by belt transects on reefs of La Parguera. Means are calculated from a total of five transect monthly observations at each reef from August 2005 to July 2006. Bars indicate 95% confidence intervals. n=60 counts/reef. Different letters represent statistical significant difference (ANOVA, p<0.05).
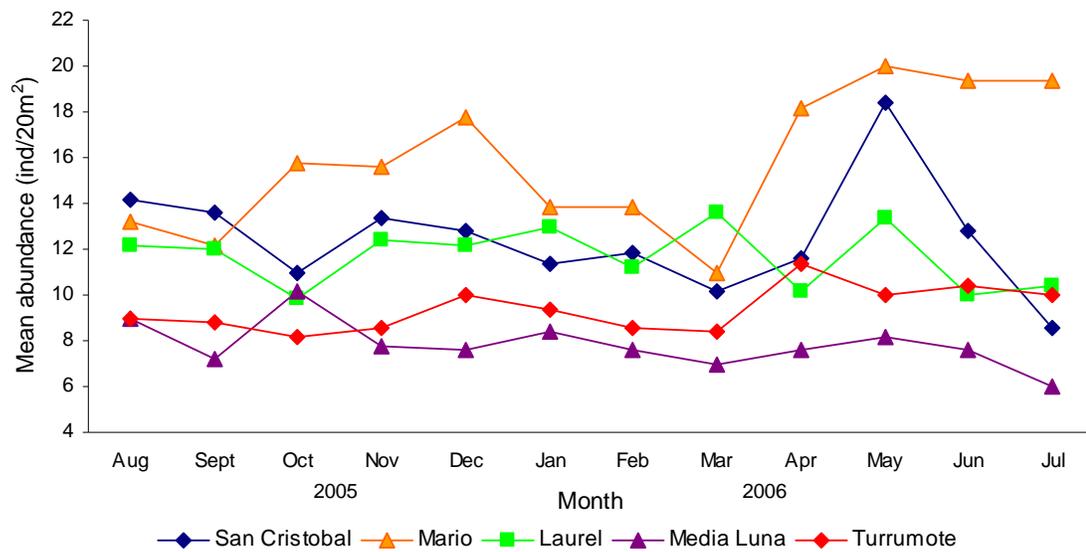
Figure 3. Monthly variations of mean abundances by *Stegastes adustus* from reefs studied at La Parguera (ANOVA, p<0.001). n=5 transects per data point.
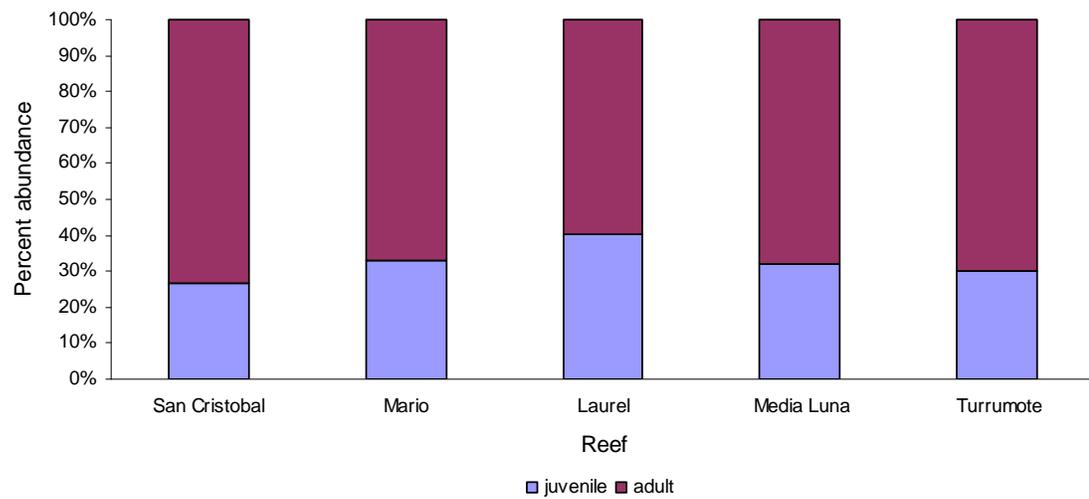
Figure 4. Mean relative abundance (%) of juvenile *Stegastes adustus* on reefs studied at La Parguera. n=300 counts per stage.
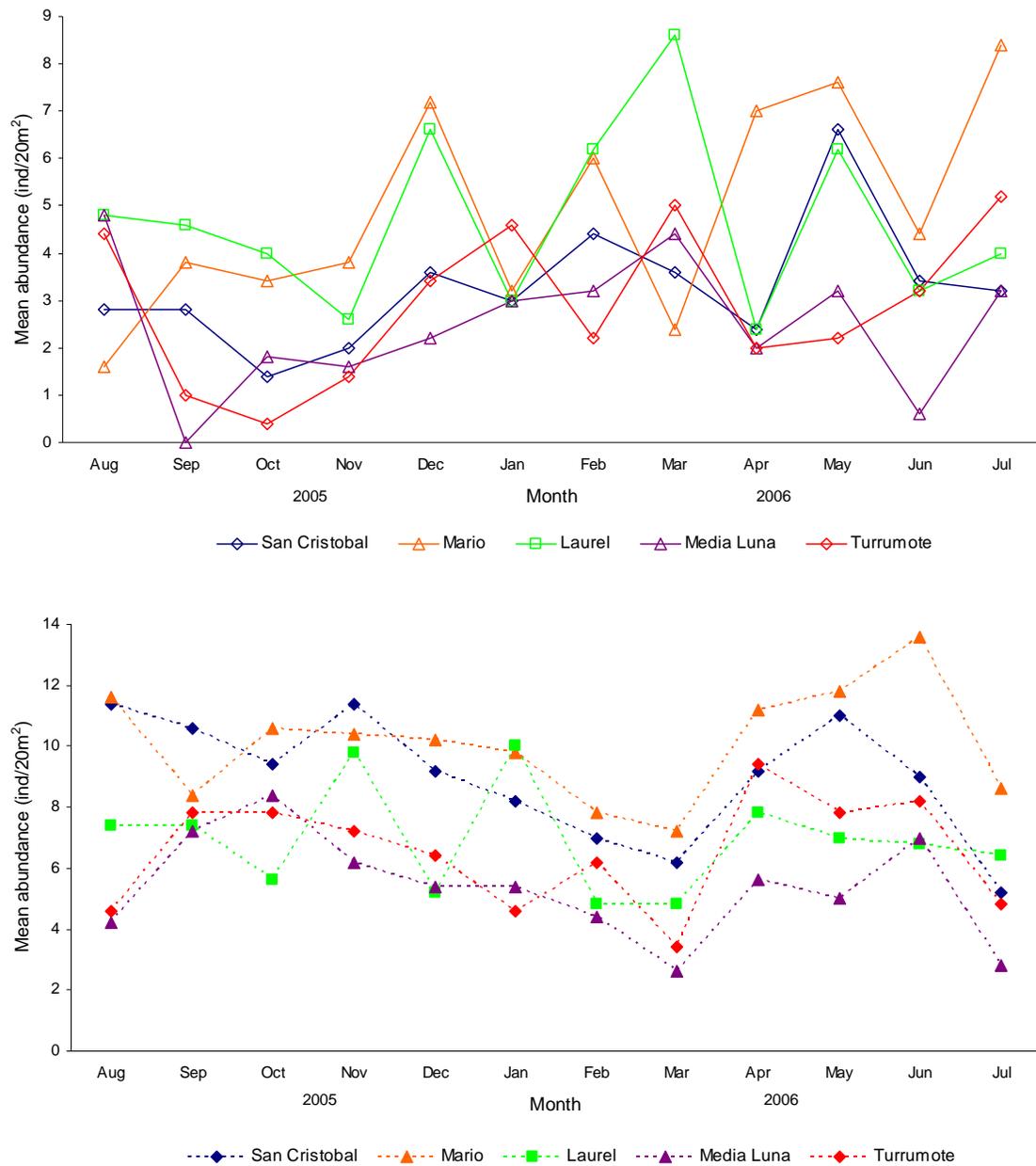
Figure 5. Monthly variations of mean abundances of juveniles (top) and adults (bottom) of *Stegastes adustus* from reefs studied at La Parguera (ANOVA, p<0.001). n=5 transects per data point.
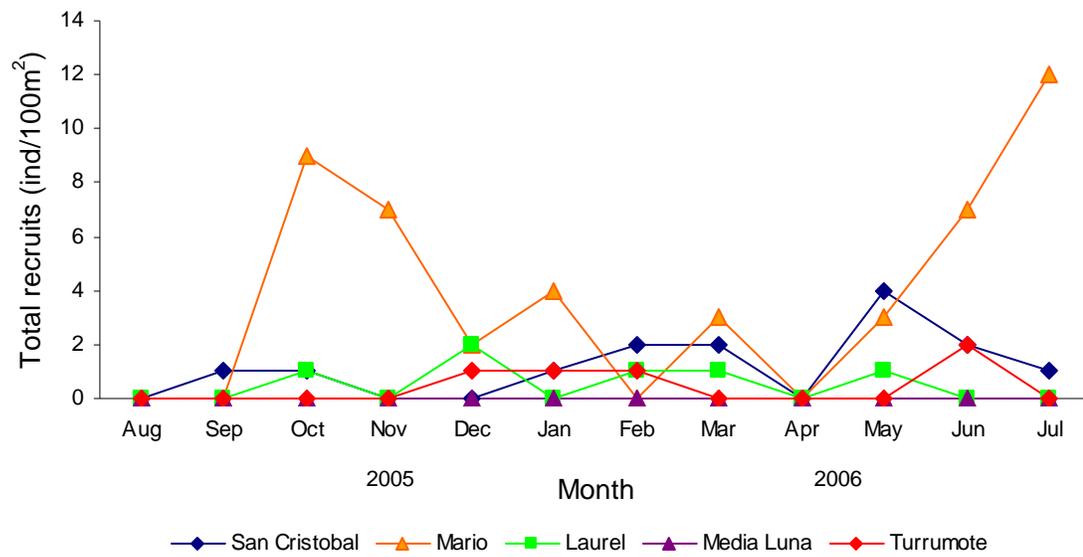
Figure 6. Monthly variations of total abundance by *Stegastes adustus* recruits from reefs surveyed at La Parguera. n=72 recruits.
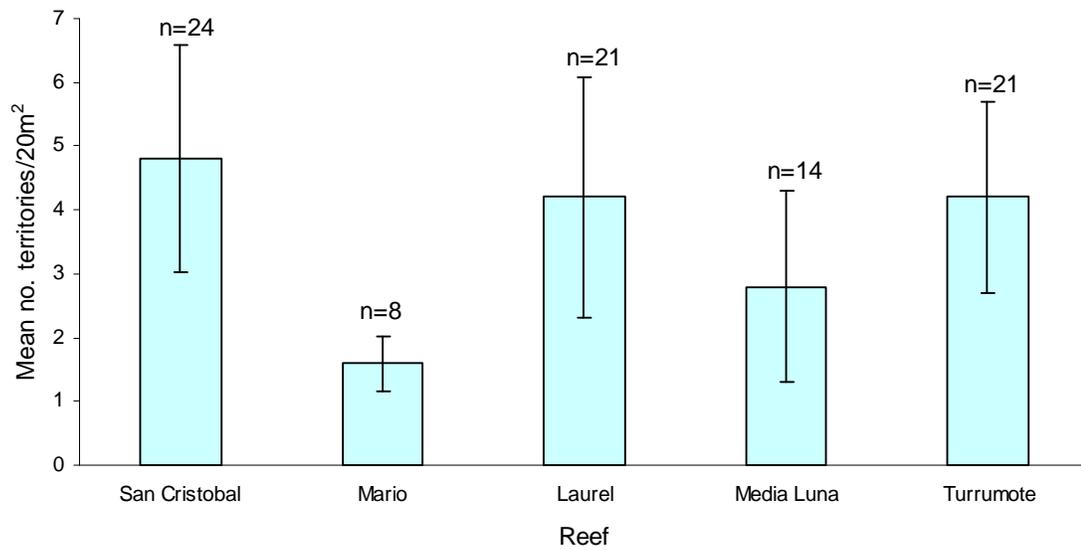
Figure 7. Mean number of *Stegastes adustus* territories in five transects per reef. Bars indicate 95% confidence intervals.
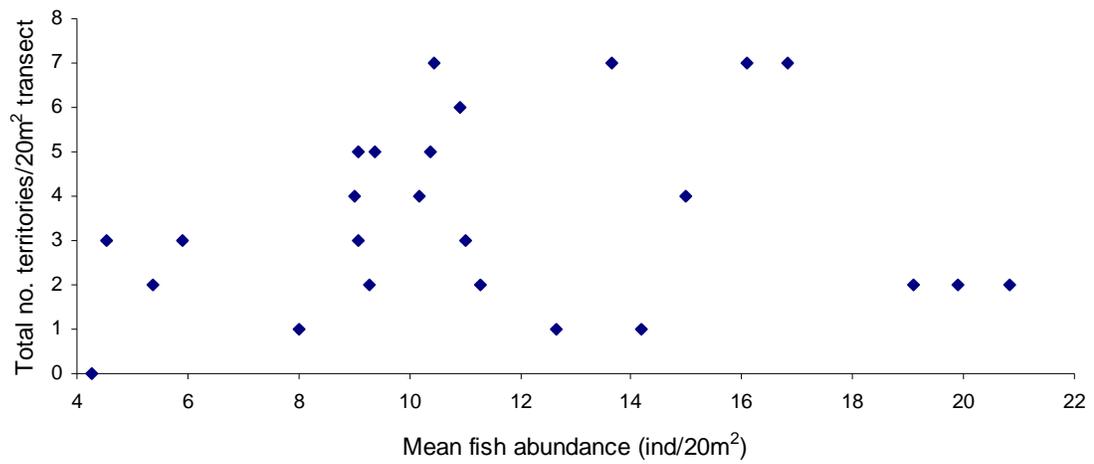
Figure 8. Relationship between mean fish abundance and total territory abundance per transect for all reefs. One territory equals one fish. n=25 transects.
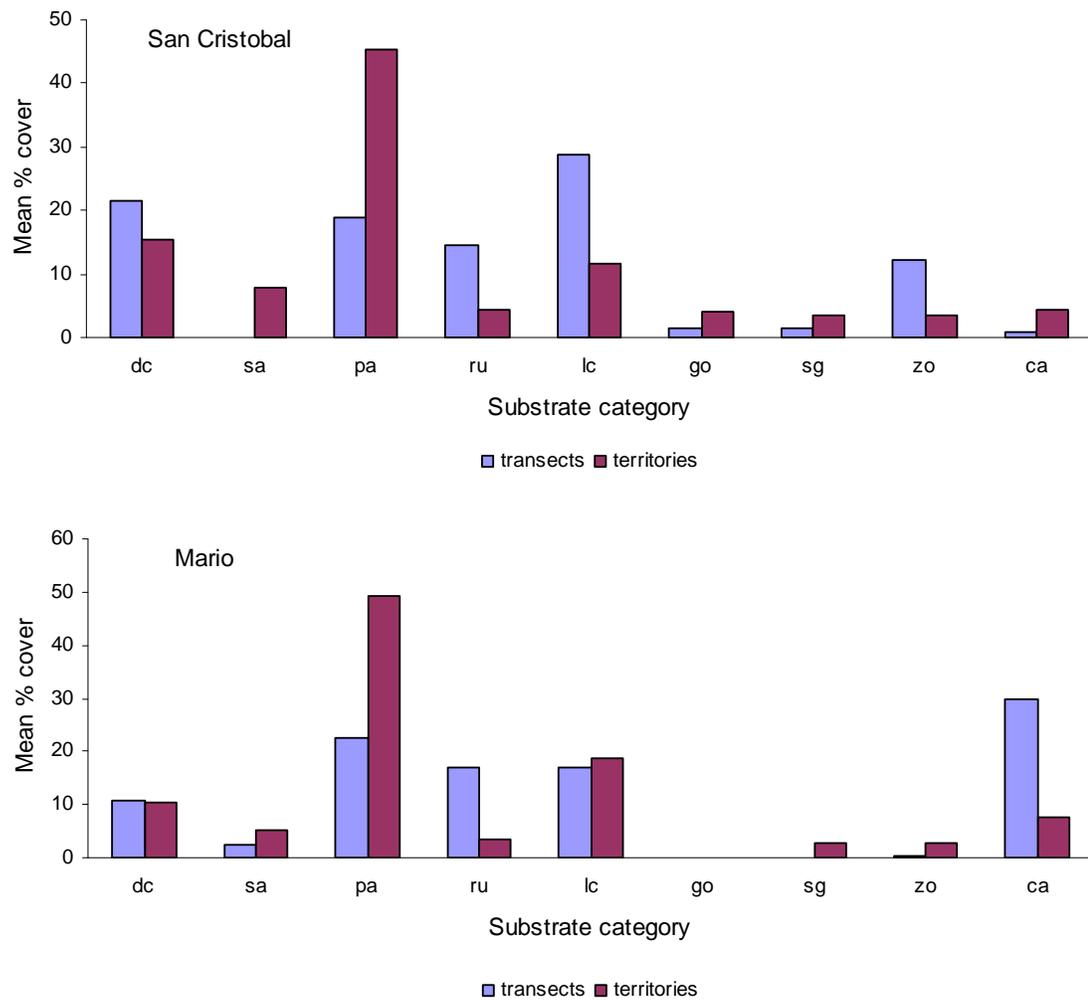
Figure 9. Distribution of mean % substrate cover in transects and territories of *S. adustus* at the reefs studied. dc-dead coral, sa-sand, pa-colonized pavement, ru-rubble, lc-live coral, go-gorgonian, sg-sea grass, zo-zoanthid, ca-calcareous algae. n=5 transects per reef, n= 0-7 territories per transect.
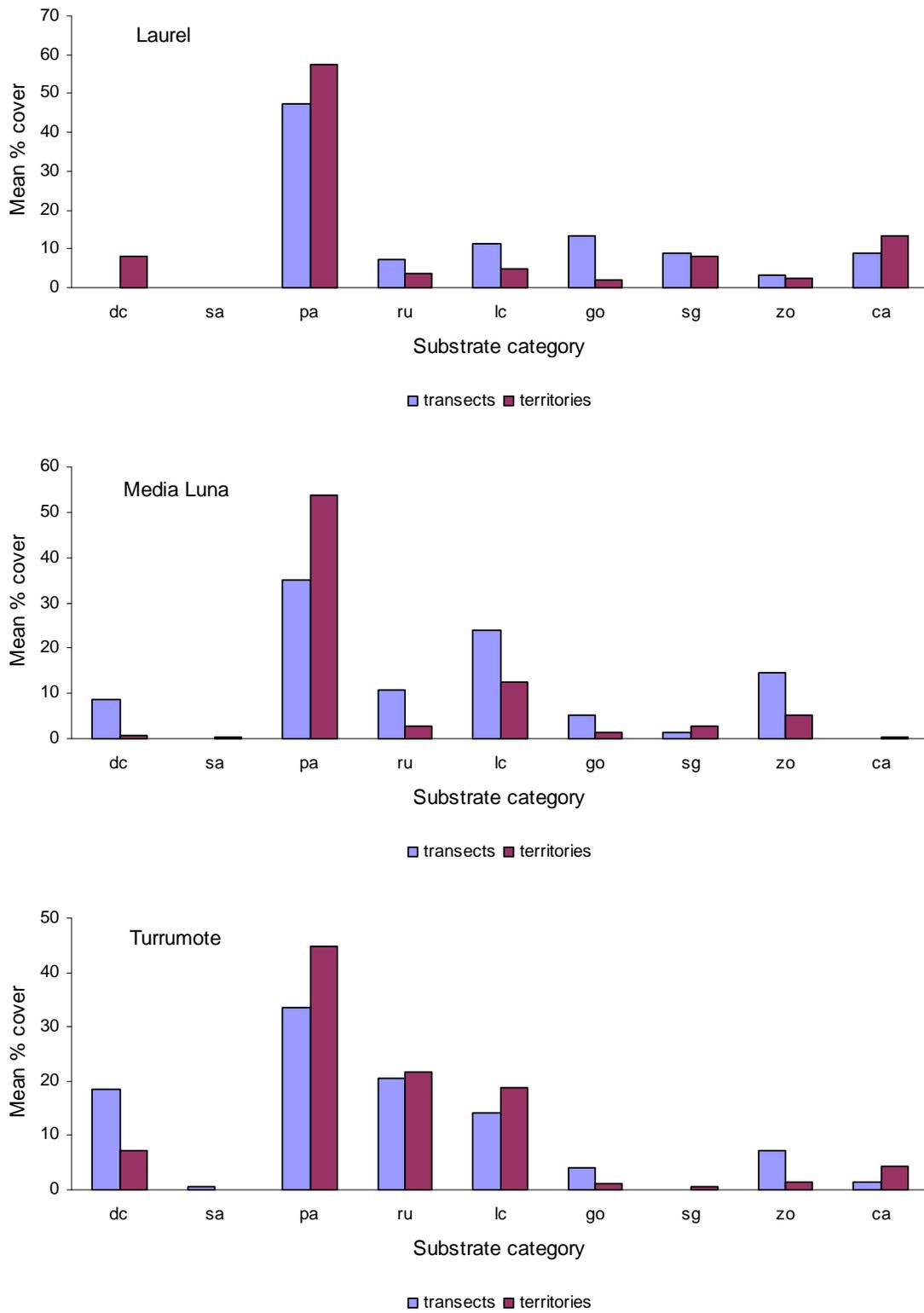
Figure 9 (continued).
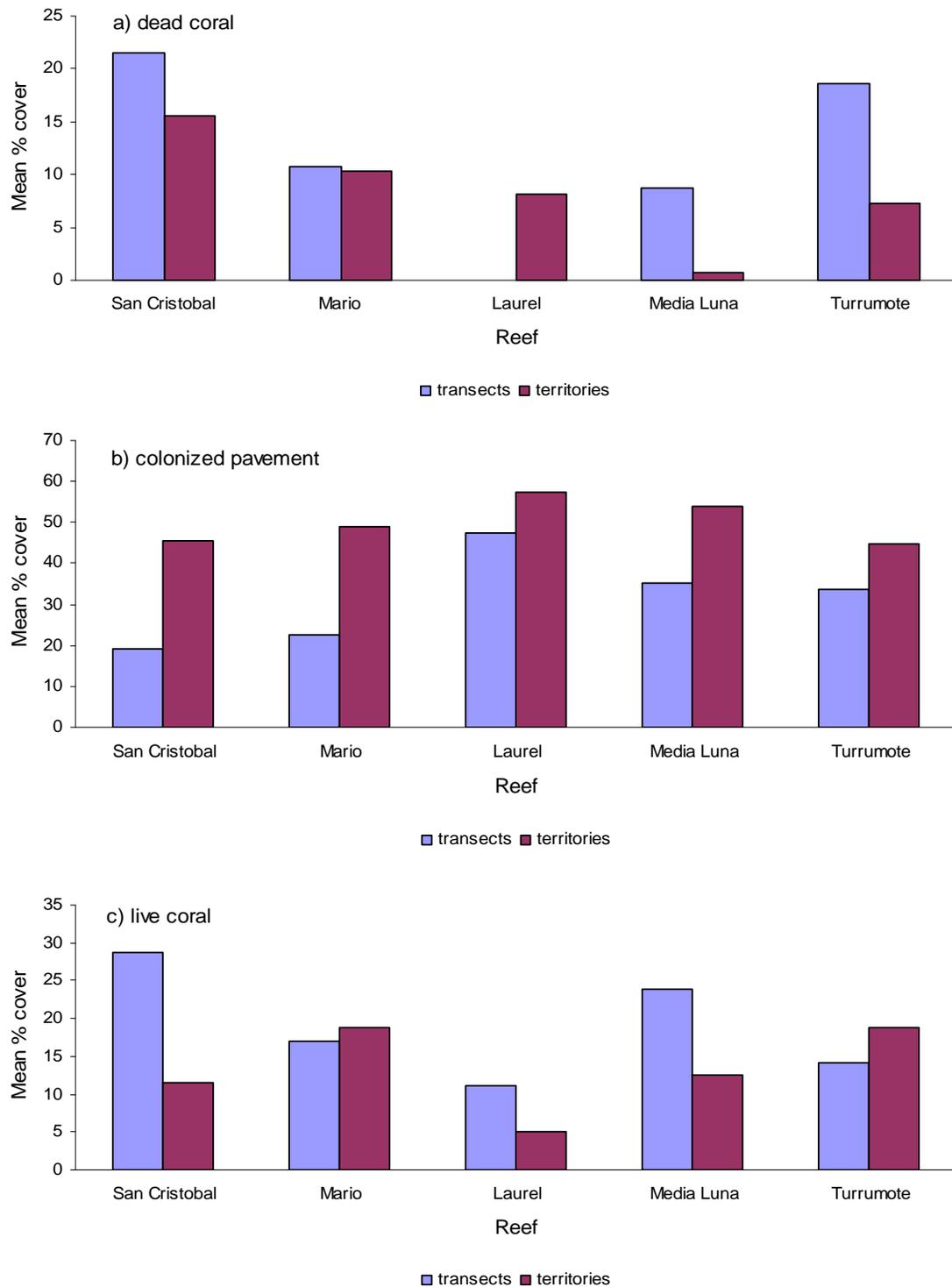
Figure 10. Mean % cover by substrate categories a) dead coral, b) colonized pavement and c) live coral on reefs studied at La Parguera from replicate transects and territories occupied by *S. adustus*. n=5 transects per reef, n= 0-7 territories per transect.
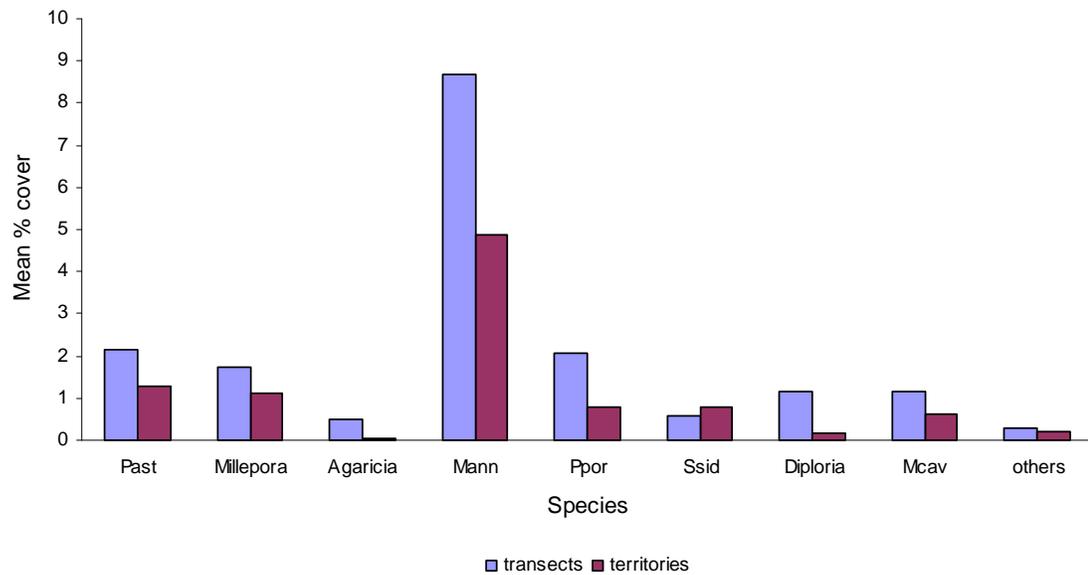
Figure 11. Comparison of the mean percent cover of coral species in transects and territories of *Stegastes adustus* among all reefs studied at La Parguera. Past-*Porites astreoides*, *Millepora* spp., *Agaricia* spp., Mann-*Montastraea annularis*, Ppor-*P. porites*, Ssid-*Siderastrea siderea*, *Diploria* spp, Mcav-*M. cavernosa*. n=25 transects, n=88 territories
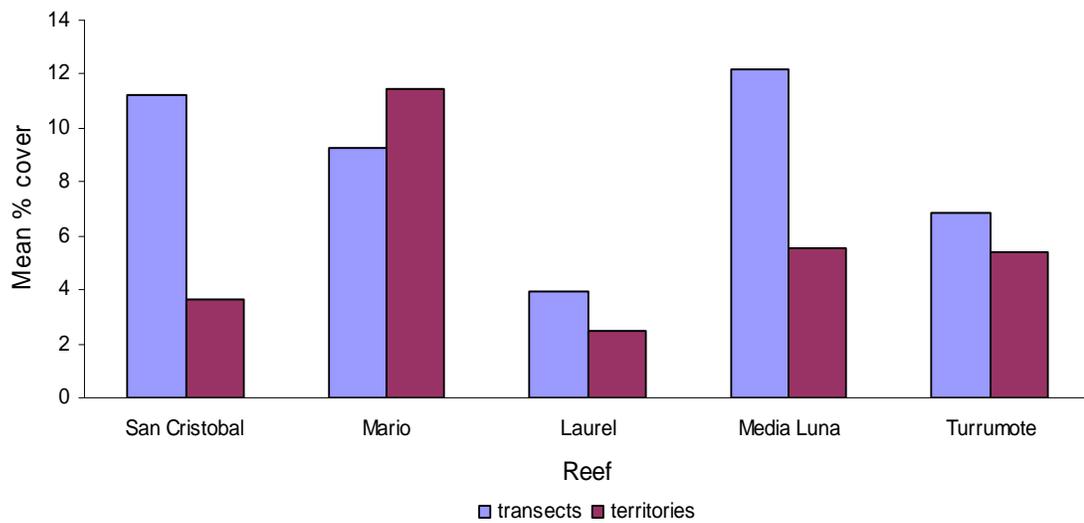
Figure 12. Comparison of the mean percent cover by *Montastraea annularis* in transects and territories of *S. adustus* between all reefs studied at La Parguera. n=5 transects per reef, n= 0-7 territories per transect per reef.
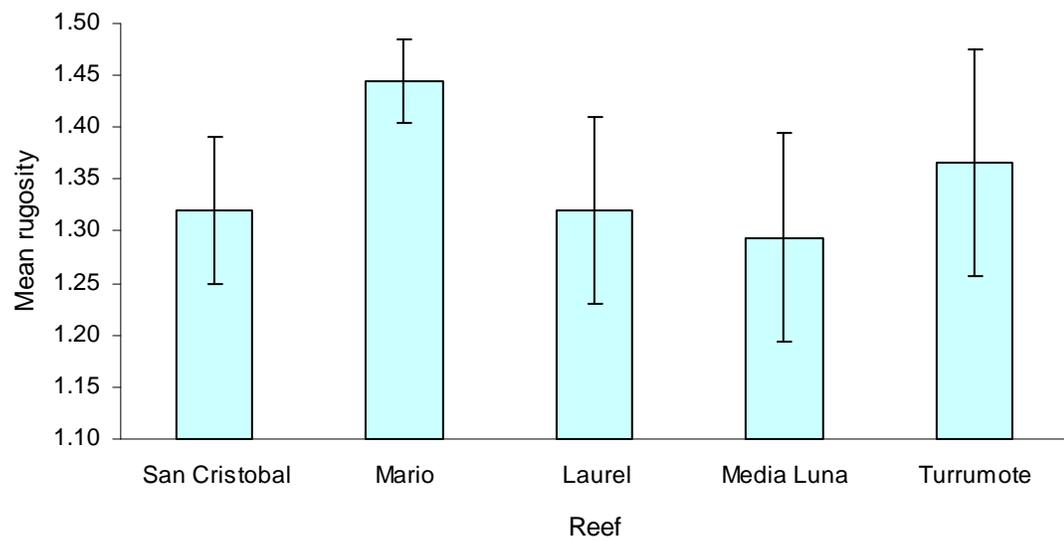
Figure 13. Mean rugosity among studied reefs at La Parguera. Bars indicate 95% confidence intervals. n=5 transects per reef.

CHAPTER 2

FACTORS AFFECTING THE DISTRIBUTION PATTERNS OF RECRUITS

INTRODUCTION

Substrate provides shelter, nesting sites, and food resources to coral reef fishes. Ecological processes influence the abundance and distribution of settlers, post-settlement recruits, juveniles and adult reef fishes. Among these factors and processes are the topographic complexity of the habitat, and the space, shelter and food availability (Cheney and Côté 2003; Jones 1991; Shulman 1984; Tolimieri 1998; Williams 1991).

Tolimieri (1998), Lirman (1994), Gutiérrez (1998) and Holbrook et al. (2000) found ontogenetic patterns of microhabitat utilization by damselfishes in the Caribbean and Pacific. Microhabitat explained approximately 85% of the abundance variation for *S. adustus* and 32 to 49% for *S. partitus* and *S. planifrons* (Tolimieri 1998). Adult *S. adustus* and *S. planifrons* showed a non-random local distribution pattern that was produced by recruits at the moment of habitat selection (Gutiérrez 1998). Similar results were observed for *Dascyllus* spp. and *S. planifrons* (Holbrook et al. 2000) and *Gobiodon* spp. (Munday 2002).

Small experimental reefs built from natural coral material, PVC pipes and empty conch shells have been used to evaluate competition, territoriality, reproductive success, effects of resource limitation, and recruitment of *Stegastes* spp. and other reef fish and reef associated species (Itzkowitz 1990; Itzkowitz and Makie 1986; Itzkowitz et al. 1995; Jones 1987, 1988; Shulman 1984; Solandt et al. 2003). In general, *Stegastes* moves to higher quality territories

when these become available. Cheney and Côté (2003) found that *S. diencaeus* recolonized vacant high quality habitats more quickly than low quality habitats.

Stegastes adustus is a territorial omnivore common in Caribbean reefs and strongly associated with the substrate. Juveniles are mostly found in sand, rubble and bare rock areas on the back reef and reef crest. Algae and small invertebrates are the top components in its diet (Randall 1967; Emery 1973). When maintaining a territory adults engage in an aggressive defense against intruding grazers (e.g. scarids, acanthurids) for their clearly visible epilithic algal mats (Foster 1985; Robertson 1984). This relatively dense lawn (~10 mm thick) traps sediments to supplement the nutritional needs of damselfish (Potts 1977).

The objective of this study was to examine microhabitat preference by recruits of the Caribbean dusky damselfish *Stegastes adustus* by means of substrate surrogates on a realistic but controlled experimental population. Such preference could explain patterns of spatial distribution in La Parguera, southwestern Puerto Rico. Food and refuge resources were manipulated in two microhabitat choice experiments involving translocation of fish to small artificial patch reefs to test the hypothesis of significant preference for shelter and/or food supply.

MATERIALS AND METHODS

Both experiments were performed during September 2007 on the back reef lagoon of San Cristóbal reef (67º 04.604' N, 17º 56.438' W), La Parguera Natural Reserve reef system in southwestern Puerto Rico (Fig. 1). The lagoon is

relatively flat and shallow. The experimental setup was located in ~2 m water depth and approximately 40 m distant from the back reef slope. The broad sandy plain provided a natural barrier against incoming reef-associated herbivores and grazers (Shulman 1984) and discouraged translocated fish outgoing towards naturally occurring coral suitable for juveniles or adults (Schmitt and Holbrook 2000). Wellington and Victor (1989) used sandy areas because small reef fishes seldom swim over open sandy areas. Any small rubble aggregations near the site were dismantled and flat-graded to avoid potential refuging of the translocated fish.

Experimental habitats were made out of small construction cinder blocks (40.0 cm L x 9.5 cm H x 19.0 cm D or 40.0 cm L x 9.5 cm H x 9.0 cm D), instead of the regular construction block (40.5 cm L x 14.0 cm H x 19.0 cm D), to build vacant experimental artificial patch reefs to be occupied by recruits. The small block has a reduced hole size, from 7.5 cm x 9.0 cm in the regular block to 3.5 cm x 8.0 cm or 4.0 cm x 8.5 cm respectively. Hixon and Beets (1993) found that a reduced block hole size (4.0 cm x 6.0 cm) attracted small-sized fish (<10 cm SL) and reduced the risk of predation.

The variability induced by shelter's opening size, water depth and habitat size (i.e., area) was eliminated by keeping those variables constant in each experiment. An enlargement in area increases reef fish recruitment abundance and species richness (Shulman 1984).

Four treatments combined the absence (-) or presence (+) of refuge (R) space (cemented holes / open holes) and food (F) resource (new blocks /

filamentous algae overgrown blocks). Blocks requiring food presence were submerged eight months in advance to allow overgrowth while blocks with food absence were cleaned everyday with a steel brush. Observations were done by SCUBA and snorkeling. The exact design and sampling protocol for each experiment is described next. I assumed that the prolongation of time spent by fish on each experimental treatment was an indication of the preference for a particular habitat at recruitment leading to spatial patterns of distribution.

Experiment 1

Twenty four *Stegastes adustus* (1.0-1.5 cm SL) were collected from the reef crest with a dip net after applying quinaldine as fish anesthetic whenever necessary (Ackerman and Bellwood 2002; Munday and Wilson 1997; Russell et al. 1978). Collection was done in the morning prior to start the experiment. Captured fish were transported to the wet lab, kept in an aerated aquarium and marked by injecting diluted tattoo ink under the scales to identify corresponding treatment and to recognize inter-block migration. Technique of color and body position for individual identification was described by Lotrich and Meredith (1974) and Malone et al. (1999), and successfully used in studies examining patterns of territorial fauna (Forrester 1990; Itzkowitz 1990; Medina-Díaz et al. 2005). Preliminary observation showed no death in a 24 hr period after injection. Fish were transported in late afternoon to the experimental site in individual plastic bags, randomly picked-up from the dive mesh bag and released to any of the six blocks of the corresponding treatment. Each treatment block received one fish.

Six replicates per treatment were distributed at random in a four by six layout with 4 m spacing between adjacent blocks (Fig. 2). A single block was used for each treatment. Daily morning surveys were conducted with SCUBA or snorkeling as needed to corroborate the presence or absence of each fish in its corresponding block. The experiment was run for five days until only one fish remained. Fish presence (i.e., check) was recorded daily. Because experimental fish could migrate all blocks were inspected every morning for movement among blocks and for settlers and new recruits from either the water column or the surroundings. The consecutive days that *S. adustus* was present on its new territory was recorded to estimate survivorship. Chi-square test was used to compare survival curves as a value of habitat suitability (Mead and Curnow 1983; Sokal and Rolf 1981). Friedman 2-way ANOVA was utilized to test for significant differences of habitat preferences.

Experiment 2

Six *S. adustus* (1.0-1.5 cm SL) were collected from the reef crest as described in experiment 1. Collection was done daily on early morning prior to the experimental run. Fish were immediately transported to the experimental site on plastic bags, randomly picked-up from the dive mesh bag and individually released to any of the six four-block artificial habitats. Each cluster received one fish.

Five replicate trials were done using six four-block clusters containing all four treatments and spaced 6 m from each other (Fig. 3). A single block was

used for each treatment. The allocation of treatments was at random for each cluster. Each cluster was surveyed four times during the daily trial to score habitat choice starting right after fish were released at 0800 and then successively at 0900, 1000 and 1100. Hourly observations (i.e., checks) were conducted by snorkeling to record the location of each fish on any of the treatments. Fish were removed at the end of daily observations, with no need of quinaldine, and released in an area 200 m north of the experimental site. The experiment was designed for non-parametric data thus Friedman 2-way ANOVA was utilized to test for significant differences of habitat choice that could explain recruitment patterns (Mead and Curnow 1983; Sokal and Rolf 1981).

RESULTS

Variations on the survivorship of recruits transferred onto experimental habitats were observed (Fig. 4). All treatments had a loss of recruits since day 1. Recruits relocated into blocks lacking refuge and food (i.e., R-F-) showed the fastest loss since all fish disappeared by day 2. A slight difference in the survivorship curve was observed between recruits assigned to blocks with absence of refuge-presence of food (i.e., R-F+) and those assigned to blocks with presence of refuge-absence of food (i.e., R+F-) and may be indicative of the importance of food regardless of refuge availability. Nonetheless, recruits on both aforementioned treatments were gone by day 3. Recruits assigned to habitats with refuge and food (i.e., R+F+) attained 16.7% survivorship at the end of the experiment on the 5th day. Survivorship among treatments was not

significantly different (X^2_1 = 11.571, df =15, p>0.05; Table 1). This result may be the effect of low sampling size to construct the survivorship curves.

There were no new fishes observed moving or recruiting into the blocks. Differences were observed in the mean (± SE) number of fish present (i.e., persisting) on each treatment during daily morning survey (i.e., check) pooled for five days. Blocks with both refuge and food recorded the highest number of checks (3.0 ± 0.8 checks), being R+F+ the only significantly different treatment (ANOVA, X^2=13.59, W=0.75, p<0.05; Fig. 5). Blocks without refuge and food had the lowest mean score (1.3 ± 1.0 checks). Habitats with no refuge but presence of food and those with presence of refuge but no food had 1.7 ± 1.0 checks and 1.5 ± 1.0 checks respectively.

Fish in experiment 2 spent time in all microhabitats (Fig. 6). The mean number (± SE) of recruits preferring a specific treatment differed significantly for the daily selection of different habitats types (ANOVA, X^2=14.62, W=0.97, p<0.05; Fig. 7). Blocks offering refuge and food had the highest mean ($\bar{x}$ ± SE) number of daily checks (11.8 ± 1.0 checks), followed by blocks lacking refuge but food present (6.6 ± 0.4 checks). Interestingly, blocks where refuge and food were absent had a higher mean number of checks (3.2 ± 0.5 checks) than those where refuge was present and food was absent (2.4 ± 0.6 checks), but the difference was not significant. Both treatments offering food were significantly different from those where food was absent.

The different sampling protocol in this experiment reduced the chances of migration and predation. In addition, the number of observations was increased thus providing a more confident result.

DISCUSSION

This study revealed a multifactorial explanation, guided by microhabitat choice, in which the patterns of abundance and distribution of recruits of *S. adustus* were determined by the availability of refuge and food. Experiment 1 showed a trend in substrate choice regardless of the few replicates while the increase in observations in experiment 2 corroborated the trend and made clear additional differences among the other treatments.

In the first experiment, even though recruits disappeared completely in three treatments, it was clear that chances of recruit persistence were affected by the substrate. The results concurred with those of substrate selection (Forrester 1990; Hixon and Beets 1989, 1993; Shulman 1984) and survival (Booth 1991) for other pomacentrid species. *Stegastes adustus* exhibited a strong relationship between abundance and habitat use when 85% of the abundance variation was explained by *Acropora* rubble (Tolimieri 1998). Adult *S. adustus* (Gutiérrez 1998) and *S. planifrons* (Gutiérrez 1998; Holbrook et al. 2000) showed that the local distribution pattern was associated with habitat selection during settlement and recruitment. Pavement has less complexity than some other substrata but contains holes and crevices used for shelter and high quality food resources that reduced the emigration of *Acanthurus bahianus* settlers which resulted in higher

abundance and persistence thus positive effect on growth and relation to patterns of juvenile distribution (Risk 1997). Strong site fidelity and high survivorship of *S. planifrons* recruits was observed in La Parguera (McGehee 1995). Even though totality of factors affecting survival of juvenile and adult dusky damselfish is not known in La Parguera, it is well documented that migration and mortality (e.g., predation) are features of relatively sedentary and territorial coral reef fishes.

Persistence refers to absence including mortality and migration. The latter was not observed in experiment 1 when swimming to detect marked recruits outside the experimental area. Rapid fish loss may be due to either mortality (e.g., predation) or migration, but predation is the preferred explanation due to the relative isolation of the experimental setup from the natural surroundings. Mortality rates in settlers and recruits are higher than in juveniles and adults. Extremely high mortality accounts for immediate fish loss after settlement, as observed in the first morning of survey in experiment 1, with a posterior sharp decline in mortality (Victor 1986). Booth and Beretta (1994) concluded that the disappearance of recruits was not due to migration but to mortality (i.e., predation) because none of the nine surviving recruits were found further than 30 cm from their initial location at subsequent censuses. Additional observations at the end of each day in experiment 1 could have lead to a better understanding of the reasons for fish loss.

Other processes during settlement and post-settlement, and behaviors like territorialism, have been found to regulate patterns of abundance and distribution

of settlers, recruits, juveniles and adult reef fishes. Among these are topographic

complexity of the habitat providing shelter from predation (Hixon 1991; Hixon

and Beets 1989, 1993), food availability (Kaufman 1977; Shulman 1984) and

density of recruits, congeners, conspecifics and predators (Tolimieri 1998;

Schmitt and Holbrook 2000). Evidence shows that available high quality

territories, those with territory features that can influence growth rates,

reproductive success, parasite loads and predation risk, or even the presence of

a nest, were reoccupied in a short time by territorial *Stegastes* (Cheney and Côté

2003; Jones 1987, 1988; Itzkowitz 1990; Itzkowitz et al. 1995; Shulman 1984).

The relationship between the abundance of adults and recruits of

Stegastes spp. has received little attention in the Caribbean regardless of its

relative higher abundance. Only Holbrook et al. (2000) obtained data to test

such relationship (r^2=0.83) between these two stages of *S. planifrons*. Studies

investigating this relationship and that between coral bleaching, overfishing, and

others should be examined to better define abundance and distribution of the

Caribbean dusky damselfish.

Because settlement and recruitment shows considerable variation on a

number of spatial and temporal scales for all tropical coral reef fishes, the

population structure may be affected by that variability (Jones 1990; Sale and

Douglas 1984; Victor 1986, 1991). While there may be a lack of pattern to

recruitment at a larger scale, this absence of pattern often disappears when the

study is scaled down. The value of these two experiments was to make an

evaluation to understand the factors influencing abundance and distribution of

new recruits and to extrapolate explanations to other life stages and species. After all, results from this study provided evidence to reject the null hypothesis and suggest that substrate selection may be controlling abundance and survival of *S. adustus*.

Table 1. Observed and expected number of translocated *Stegastes adustus* recruits for each treatment in experiment # 1. Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F).

Day	Treatments							
	R-F-		R-F+		R+F-		R+F+	
	obs	exp	obs	exp	obs	exp	obs	exp
0	6	4.3	6	5.3	6	4.8	6	9.6
1	2	1.8	2	2.2	2	2.0	4	4.0
2	0	1.1	2	1.3	1	1.2	3	2.4
3	0	0.5	0	0.7	0	0.6	3	1.2
4	0	0.2	0	0.2	0	0.2	1	0.4
5	0	0.2	0	0.2	0	0.2	1	0.4

Figure 1. Location of San Cristobal reef within La Parguera Natural Reserve reef system in southwestern Puerto Rico and the experimental site on the back reef lagoon.

R+F-   R+F+   R-F+   R+F+   R+F+   R+F+

R-F-   R-F+   R+F+   R-F-   R+F-   R-F+

R+F+   R+F-   R+F-   R+F-   R-F+   R-F-

R-F+   R-F-   R-F-   R-F+   R-F-   R+F-
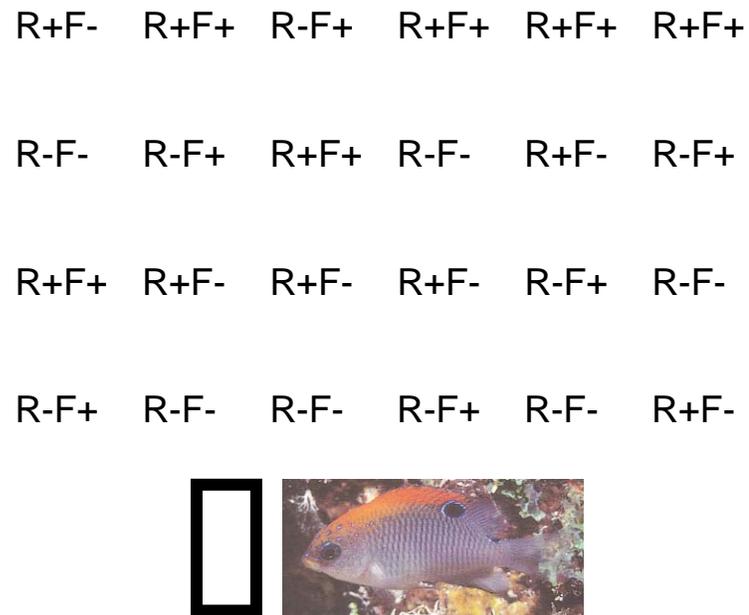
Figure 2. Random layout of treatments for experiment # 1. Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F).

R-F-

R-F+ R+F+

R+F-
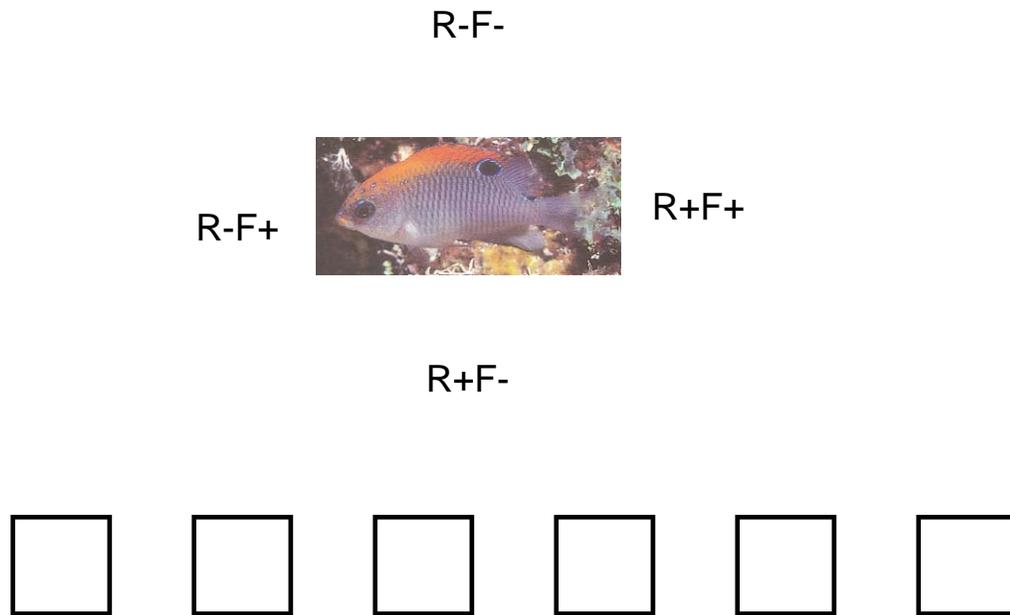
Figure 3. Treatment arrangement of experiment # 2. Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F).
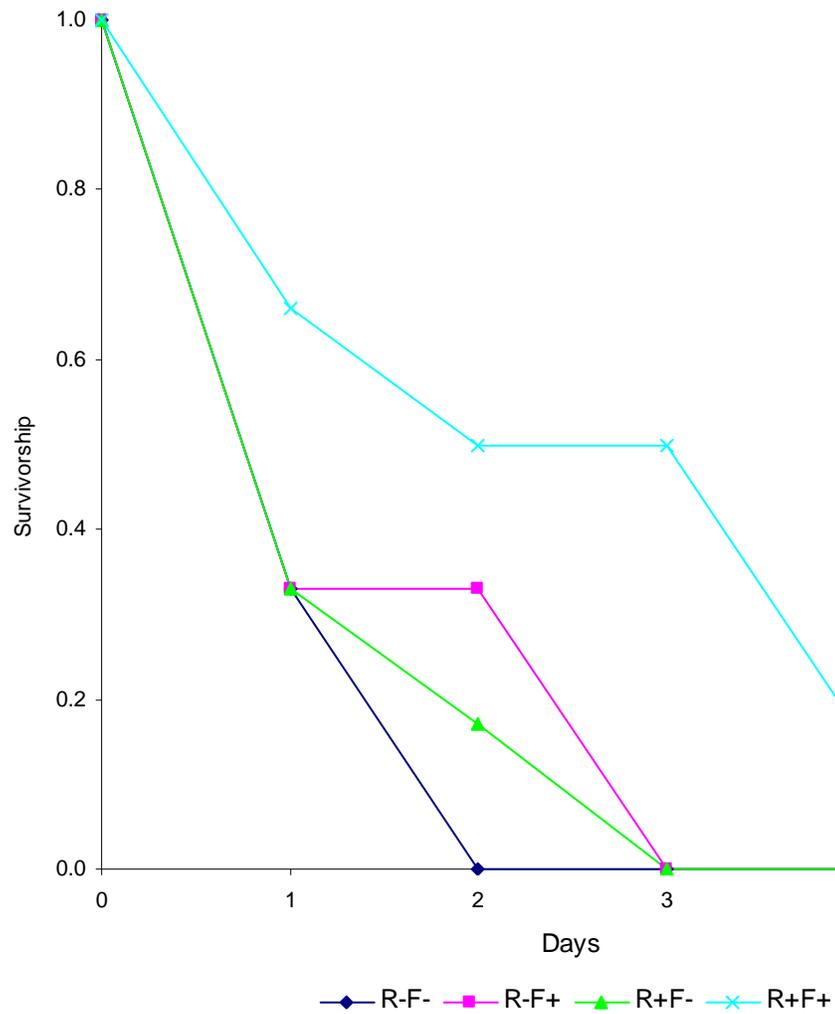
Figure 4. Survivorship of *Stegastes adustus* on the four treatments: R-F-, R-F+, R+F-, R+F+ (X^2_1 = 11.571, df =15, p>0.05). Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F).
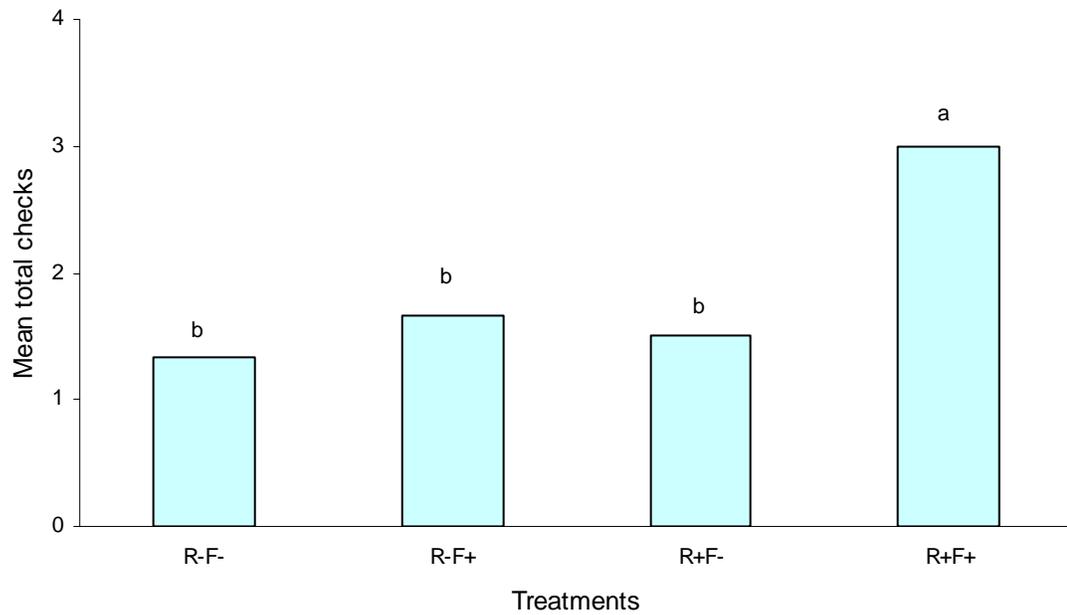
Figure 5. Mean number of daily checks per treatment (p<0.05). Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F). Letters indicate significant differences among treatments.
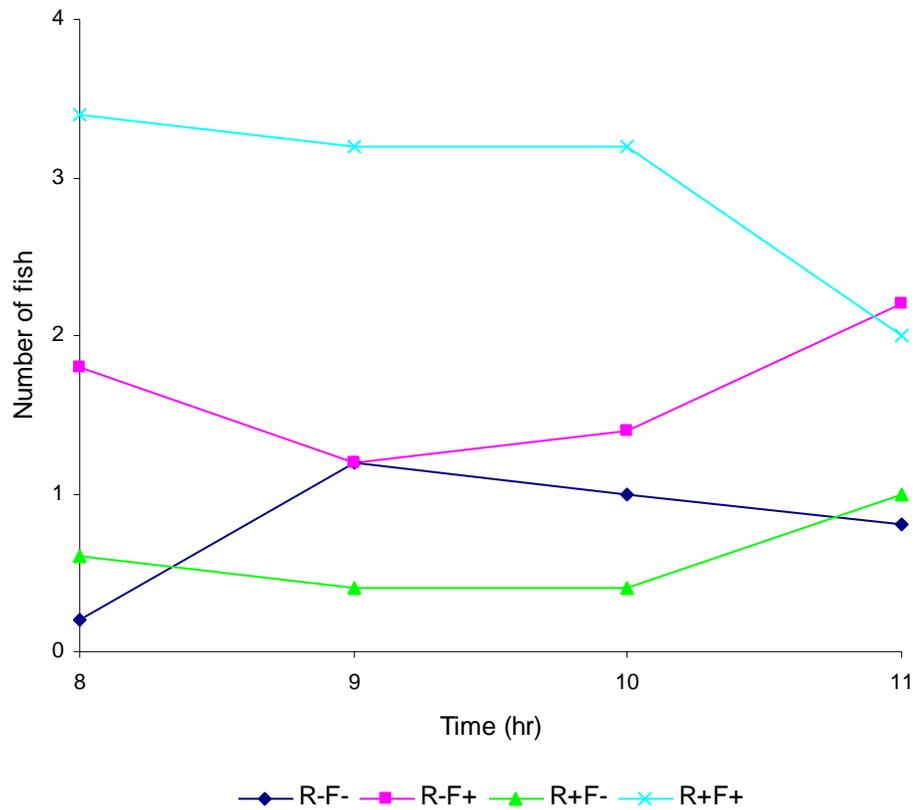
Figure 6. Mean number of fish observed in each treatment during hourly observations. Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F).
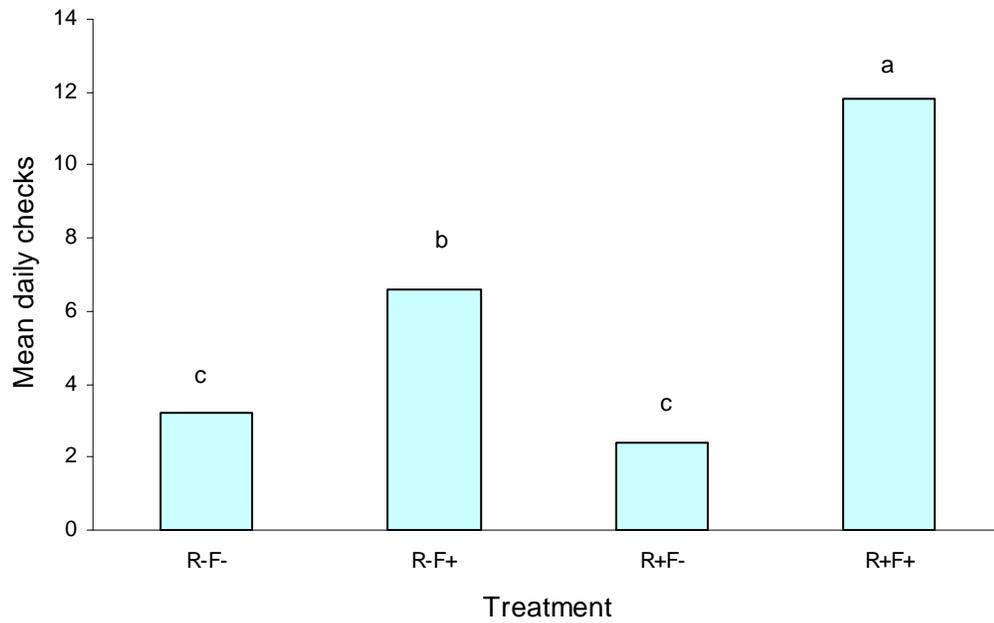
Figure 7. Mean number of daily checks per treatment (p<0.05). Treatments consisted of absence (-) or presence (+) of refuge (R) and food (F). Letters indicate significant differences among treatments.

CONCLUSIONS

Spatial and temporal differences in abundance and distribution of the dusky damselfish, *Stegastes adustus* were manifested in this study and were similar to those reported elsewhere in the Caribbean and Western Atlantic. Spatial and temporal differences of abundances for juveniles and adults, and for recruits may be explained by ecological processes like ontogenetic shift, habitat associations and priority effects thus allowing coexistence.

Differences were not observed in the number of territories per site. Mario showed the lowest amount of territories, in contrast to the high fish abundance observed there.

Colonized pavement was the most extensive reef substrate cover category but no association with abundance and distribution of *S. adustus* was observed. On the other hand, abundance and distribution were positively associated to less covering substrate categories such as calcareous algae, but negatively related to cover by zoanthids and gorgonians. Live coral species, particularly boulder star coral, *M. annularis* and rugosity were not different among reefs and had no effect on the abundance and distribution of *S. adustus*. Reef substrate cover by dead coral was positively associated to the number of established territories.

Multi-factorial experiments from this study suggest that patterns of abundance and distribution for recruits of *S. adustus* are regulated by substrate attributes, such as the availability of refuge and food. The rejection of the null hypothesis suggests that substrate selection may be controlling abundance and

survival of *S. adustus*. This association has a high potential to determine the abundance and distribution of juveniles and adults of the species.

This study shows that *S. adustus* is an opportunistic generalist that settles and recruits to a specific habitat, but that juveniles and adults may further benefit from modifying their surroundings. Setting aside variability in settlement, environmental factors and other biological and ecological processes may explain the observed differences in the abundance and distribution of *S. adustus*.

There is a need to increase the studies on *Stegastes* species. The relationship between the abundance of adults and recruits of *Stegastes* spp. has received little attention in the Caribbean, understanding the population dynamics is significant for the species.

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Appendix A.1. Result of the repeated measures 2-way ANOVA for the comparison of the mean abundance of *S. adustus* at La Parguera.

Source	df	SS	MS	F	p
reef	4	2259.153	564.788	3.235	0.040
month	11	279.077	25.371	4.066	<0.001
reef x month	44	779.007	17.705	2.461	<0.001
residual	176	1266.127	7.194		
Total	299	8428.437	28.189		

Appendix A.2. Result of the three-way ANOVA for the comparison of the mean abundance of *S. adustus* in studied reefs at La Parguera.

Source	df	SS	MS	F	p
stage	1	816.966	816.966	2.695E+016	<0.001
month	11	55.815	5.074	1.674E+014	<0.001
reef	4	451.831	112.958	3.726E+015	<0.001
stage x month	11	295.922	26.902	8.874E+014	<0.001
stage x reef	4	81.404	20.351	6.713E+014	<0.001
month x reef	44	155.801	3.541	1.168E+014	<0.001
stage x month x reef	44	235.188	5.345	1.763E+014	<0.001
Residual	120	3.638E-12	3.032E-14		
Total	239	2092.927	8.757		

Appendix A.3. Result of the two-way repeated measures ANOVA for the comparison of the mean abundance of a) juveniles and b) adults of *S. adustus* in studied reefs at La Parguera.

a) juveniles

Source	df	SS	MS	F	P
reef	4	299.587	74.897	1.489	0.252
month	11	337.317	30.665	5.585	<0.001
reef x month	44	474.333	10.780	2.221	<0.001
residual	176	858.167	4.876		
Total	299	3170.837	10.605		

b) adults

Source	df	SS	MS	F	P
reef	4	891.720	222.947	3.392	0.034
month	11	525.867	47.806	8.558	<0.001
reef x month	44	401.333	9.121	1.922	0.002
residual	176	835.333	4.746		
Total	299	4345.387	14.533		

Appendix A.4. Result of the one-way ANOVA for the comparison of the mean number of territories of *S. adustus* in studied reef at La Parguera.

Source	df	SS	MS	F	p
reef	4	33.84	8.46	2.274	0.097
residual	20	74.40	3.72		
Total	24	108.24			

Appendix A.5. Result of the two-way ANOVA for the comparison of the mean percent substrate cover types in transects and territories of *S. adustus* in studied reefs at La Parguera: a) San Cristobal, b) Mario, c) Laurel, d) Media Luna and e) Turrumote.

a) San Cristobal

Source	df	SS	MS	F	p
substrate	8	8628.144	1078.518	14.381	<0.001
location	1	0.000	0.000	0.000	1.000
substrate x location	8	3229.139	403.642	5.382	<0.001
Residual	72	5399.839	74.998		
Total	89	17257.122	193.900		

b) Mario

Source	df	SS	MS	F	p
substrate	8	10748.433	1343.554	14.283	<0.001
location	1	1.455E-011	0.000	0.000	1.000
substrate x location	8	3519.382	439.923	4.677	<0.001
Residual	72	6772.764	94.066		
Total	89	21040.579	236.411		

c) Laurel

Source	df	SS	MS	F	p
substrate	8	20002.045	2500.256	24.965	<0.001
location	1	0.000	0.000	0.000	1.000
substrate x location	8	919.057	114.882	1.147	0.343
Residual	72	7210.776	100.150		
Total	89	28131.879	316.089		

d) Media Luna

Source	df	SS	MS	F	p
substrate	8	15962.295	1995.287	21.173	<0.001
location	1	111.111	111.111	1.179	0.281
substrate x location	8	1673.353	209.169	2.220	0.036
Residual	72	6784.928	94.235		
Total	89	24531.687	275.637		

e) Turrumote

Source	df	SS	MS	F	p
substrate	8	13430.517	1678.815	11.729	<0.001
location	1	0.000	0.000	0.000	1.000
substrate x location	8	807.805	100.976	0.705	0.686
Residual	72	10305.557	143.133		
Total	89	24543.879	275.774		

Appendix A.6. Result of the two-way ANOVA for the comparison of the mean percent substrate cover by a) dead coral, b) colonized pavement and c) live coral by transects and territories of *S. adustus* in studied reefs at La Parguera.

a) dead coral

Source	df	SS	MS	F	P
reef	4	1438.437	359.609	2.712	0.043
location	1	153.053	153.053	1.154	0.289
reef x location	4	581.290	145.323	1.096	0.372
Residual	40	5303.381	132.585		
Total	49	7476.162	152.575		

b) colonized pavement

Source	df	SS	MS	F	P
reef	4	2486.548	621.637	1.901	0.129
location	1	4317.869	4317.869	13.204	<0.001
reef x location	4	634.133	158.533	0.485	0.747
Residual	40	13080.292	327.007		
Total	49	20518.842	418.752		

c) live coral

Source	df	SS	MS	F	p
reef	4	888.619	222.155	1.626	0.187
location	1	398.622	398.622	2.917	0.095
reef x location	4	815.530	203.882	1.492	0.223
Residual	40	5466.296	136.657		
Total	49	7569.068	154.471		

Appendix A.7. Result of the two-way ANOVA for the comparison of the mean percent cover of live coral species in transects and territories of *S. adustus* in studied reefs at La Parguera.

Source	df	SS	MS	F	p
species	7	350.910	50.130	20.916	<0.001
location	1	16.525	16.525	6.895	0.011
species x location	7	16.271	2.324	0.970	0.461
Residual	64	153.394	2.397		
Total	79	537.100	6.799		

Appendix A.8. Result of the two-way ANOVA for the comparison of the mean percent cover of *M. annularis* in transects and territories of *S. adustus* in studied reefs at La Parguera.

Source	df	SS	MS	F	p
reef	4	60.379	15.095	1.819	0.288
location	1	22.207	22.207	2.676	0.177
Residual	4	33.193	8.298		
Total	9	115.778	12.864		

Appendix A.9. Result of the one-way ANOVA for the comparison of the mean rugosity in studied reef at La Parguera.

Source	df	SS	MS	F	p
reef	4	0.070	0.017	1.841	0.161
residual	20	0.190	0.009		
Total	24	0.260			