

Recruitment and habitat selection of newly settled *Sparisoma viride* to reefs with low coral cover

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ABSTRACT: Live scleractinian corals are a prime microhabitat for many recruiting coral reef fishes, yet live coral cover has exhibited widespread declines, and the impact of this loss on recruiting fishes is not well understood. Although reduced recruitment rates of parrotfishes (Scaridae) have been observed after loss of coral cover, increased juvenile parrotfish abundance observed in connection with increased macroalgal abundance on reefs suggests that some parrotfish may be capable of utilizing macroalgae as recruitment microhabitat. To test this hypothesis, recruitment rates of newly settled stoplight parrotfish *Sparisoma viride* were measured on reefs in the upper Florida Keys that have lost much of their coral cover. Although *S. viride* has previously been shown to strongly associate with the branching coral *Porites porites* on Caribbean reefs, we found that on reefs with low coral cover, *S. viride* occurred most frequently in areas of high cover of the macroalgae *Dictyota* spp. Further, this microhabitat association scaled up such that reefs with increasing macroalgal cover (up to ~16%) supported greater densities of juvenile *S. viride*. At higher levels of *Dictyota* spp. (>16% cover), site-specific *S. viride* recruitment leveled off, suggesting the influence of other processes such as differential larval supply. These results indicate that newly settled stoplight parrotfish are able to utilize the increased macroalgal cover associated with loss of coral cover and that this microhabitat may provide an alternative recruitment refuge.

KEY WORDS: *Sparisoma viride* · Microhabitat selection · Recruitment · Macroalgae

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INTRODUCTION

Many reef fishes are closely associated with specific components of the benthos; consequently, reef fish population and community structure can be influenced by the distribution and availability of these microhabitats (Bell & Galzin 1984, Carr 1994, Halford et al. 2004). For some reef fishes, selection of specific microhabitats occurs soon after settlement to the reef from the pelagic larval stage, so the spatial distribution of these microhabitats can be a strong determinant of the magnitude and spatial distribution of recruitment (Tolimieri 1998b, Holbrook et al. 2000). Although microhabitats selected by settling fishes are often not retained by adult fishes, the dynamics that occur during recruitment can influence the distribution and abundance of adult fish (Tolimieri 1998b, Holbrook et al. 2000) and

thus can be an important aspect of population regulation. On coral reefs, the composition and distribution of live corals have been found to influence both recruit and adult populations of many fish species (Bell & Galzin 1984, Tolimieri 1998b, Holbrook et al. 2000, Halford et al. 2004). However, notable declines in live coral cover have occurred on many reefs in recent decades (Gardner et al. 2003), and the uncertainty regarding the ability of these reefs to recover raises questions about how this loss of habitat will affect reef fish populations. While some reef fishes can be highly resistant to benthic disturbances (Halford et al. 2004), others have been shown to be vulnerable to the point of extinction (Dulvy et al. 2003, Jones et al. 2004). Declines in fish populations may be particularly destabilizing in the Caribbean region due to relatively low species diversity within each fish guild (Bellwood et al. 2004).

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The herbivorous fish guild performs a major role in coral reef communities by maintaining algae in a state of low biomass and high production (Lewis 1986). Among parrotfishes (Scaridae), newly settled juveniles are frequently site-attached and associated with specific microhabitats (Bellwood & Choat 1989, Tolimieri 1998b), including particular scleractinian corals (Bellwood & Choat 1989, Tolimieri 1998b). The impact of changes in benthic community composition on scarid settlement and recruitment rates appears variable; although decreased scarid recruitment has been observed following heavy loss of coral cover (Doherty et al. 1997), increased juvenile abundance has been noted with increased macroalgal cover (Carpenter 1990). The association of some juvenile scarid species with macroalgal patches (Sale et al. 1984, Bellwood & Choat 1989, Carpenter 1990) suggests that scarids may be plastic in their microhabitat use and capable of successfully utilizing macroalgae when preferred live coral microhabitats are limited.

The present study was designed to investigate the recruitment dynamics of an important reef herbivore, the stoplight parrotfish *Sparisoma viride*, on reefs which have lost a majority of their coral cover. *S. viride* has been found to select for the branching coral *Porites porites*, as recruitment microhabitat and this habitat association has been shown to scale up to adult fish distribution patterns (Tolimieri 1998b). The Florida Keys reef tract has experienced notable declines in live coral cover and currently has among the lowest coral covers in the Caribbean region (Porter & Meier 1992).

The specific objectives of the present study were to: (1) measure temporal and spatial variation in *S. viride* recruitment to inshore and offshore reefs in the upper Florida Keys and (2) determine whether newly settled *S. viride* (<20 mm total length, TL) exhibit microhabitat selection on reefs with low live coral cover (<15%) and high macroalgal cover (10 to 35%).

MATERIALS AND METHODS

Recruitment surveys. Recruitment surveys were conducted monthly for 2 consecutive years beginning in April 2003 and ending in March 2005 (YR1: April 2003 to March 2004; YR2: April 2004 to March 2005). Surveys were conducted during the low settlement period (the week of full moon) (D'Alessandro et al. 2007) each month in order to include only recruits that had settled within the previous month. Two replicate reefs of each of 3 reef types in the upper Florida Keys were sampled (Fig. 1). The 3 reef types were high relief (spur and groove) offshore reefs (FR: French; MO: Molasses), low relief (relict) offshore reefs (SI: Sand Island; PI: Pickles), and inshore patch reefs (WB: White Banks; TG: Triangles). The high relief reefs were also Sanctuary Protection Areas (SPAs), protected from all take since 1995. At each site, all newly recruited scarids (<20 mm TL) were counted in fifteen 5 × 1 m transects, but for the purposes of the present study, we focused on *Sparisoma viride*, the stoplight parrotfish. Transects were laid haphazardly on the

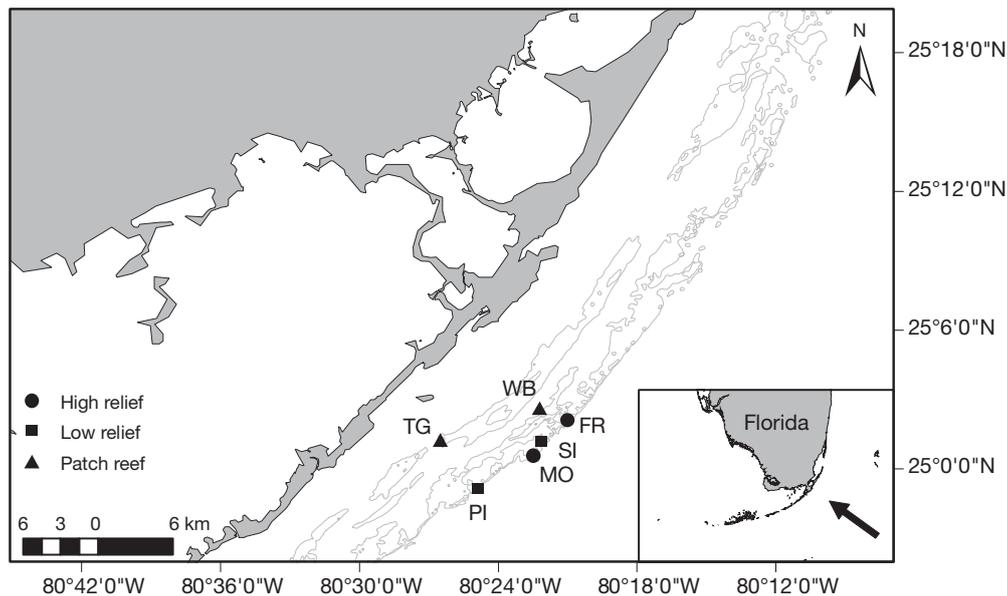


Fig. 1. Study sites in the upper Florida Keys, USA, consisting of high relief offshore reefs: French (FR), Molasses (MO); low relief offshore reefs: Sand Island (SI), Pickles (PI); and inshore patch reefs: White Banks (WB), Triangles (TG)

reef, and scarids were counted by 2 divers, each surveying a 0.5 m wide swath to either side of the transect tape. All holes and overhangs were examined, and the substrate was lightly fanned in order to detect all new recruits on the benthos.

Microhabitat selection. Microhabitat use by *Sparisoma viride* recruits was examined monthly for 6 consecutive months from April through October 2003. Microhabitat surveys were conducted concurrently with recruitment surveys on the same transects. Each diver carried several small, flagged fishing weights and a 0.25 × 0.25 m quadrat containing a grid of intersecting lines. The small quadrat size was chosen on the basis of a pilot study and observations of extremely restricted movement range of new scarid recruits. When a *S. viride* recruit was encountered on a transect, a weight was dropped in the exact spot the fish was first seen. After the recruitment survey of each transect was complete, a quadrat was centered over each of the marked spots plus 3 random points along the transect. Percent cover of substratum characteristics (e.g. coral cover and algal cover) within each quadrat was measured by recording the substratum characteristics at 20 points determined by intersections of lines on the quadrat. Algal turf was defined as filamentous algae ≤10 mm in height. Macroalgae was defined as foliose algae >10 mm height and was recorded to genus if possible. Height of benthic algae was measured to the nearest 1 mm using a plastic ruler. Rugosity within each quadrat was measured by laying a length of a fine-link chain (10 mm links) along the contour of the substrate across the diagonal of the quadrat and comparing the length of chain to the linear distance of the quadrat diagonal.

Data analyses. A generalized linear mixed-model with log-link and Poisson distribution was used to determine whether recruitment varied among years, months, reef types, and sites. Site was a random factor and was nested in reef type; all other factors were fixed. Zero data were transformed to (0 + 0.1). All model assumptions were verified. To test for the effect of sites in the model, the difference between the -2 res log likelihood values for the full model and model excluding sites was tested against a chi square distribution. To examine whether monthly patterns of recruitment differed between years, a 2-sample Kolmogorov-Smirnov test was used to test for differences in distributions of monthly means between years.

A 2-way multivariate analysis of variance (MANOVA, site and quadrat-type as factors) was used to test for differences in substratum characteristics among sites and between null and *Sparisoma viride* quadrats. Macroalgal cover was analyzed in 3 separate groups: the 2 most common genera, *Dicyota* spp. and *Halimeda* spp., and 'other macroalgae' (all other

macroalgal genera). An arcsin square-root transformation of substratum data was used to homogenize variances. Univariate *F*-tests were used to identify the specific substrata that varied among sites and between null and occupied quadrats. Significantly higher occurrence of substratum characteristics within occupied quadrats indicated selection for those particular substrate characteristics (i.e. microhabitats are occupied more frequently than expected).

To test whether microhabitats selected for on small spatial scales scaled up to recruitment patterns on larger spatial scales, mean percent cover of selected microhabitats were calculated for each site, using data from randomly located (null) quadrats only. Linear and non-linear (logistic, exponential, and asymptotic) relationships were calculated for mean densities of *Sparisoma viride* recruits at each site during the 6 mo microhabitat study versus site-specific microhabitat characteristics, and best-fit models were selected on the basis of explanatory power and significance.

RESULTS

Temporal and spatial patterns in recruitment

Density of *Sparisoma viride* recruits differed significantly among the fixed factors (year and months), but not among reef types (Table 1). The effect of the random factor (site) had a high covariance estimate (0.7439), indicating that sites were responsible for substantial variation in the model. The difference between the -2 res log likelihood values for the full model and model excluding sites tested against a chi square distribution was significant ($p < 0.05$). All other random factors (interaction effects with site) had zero covariance estimates so were dropped from the model to increase power to detect main effects. Higher numbers of *S. viride* recruits were observed at all sites in YR1 compared to YR2 (Fig. 2); however, the monthly pattern of recruitment was not significantly different

Table 1. Results of partially nested mixed-model ANOVA on *Sparisoma viride* recruitment over 2 yr (2003 to 2005) to 6 sites representing 3 reef types in the upper Florida Keys. Type 3 tests of fixed effects

Effect	df	<i>F</i>	<i>p</i>
Year	1, 60	15.16	0.0003
Month	11, 60	7.61	<0.0001
Reef type	2, 3	1.77	0.3113
Year × Month	11, 60	0.75	0.6881
Year × Reef type	2, 60	1.74	0.1843
Year × Month × Reef type	20, 60	1.43	0.1433

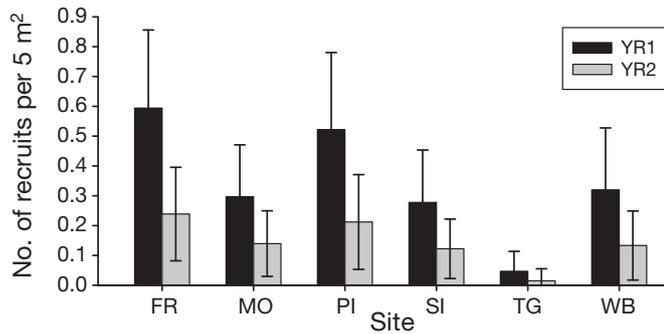


Fig. 2. *Sparisoma viride*. Annual mean (\pm SE) number of stoplight parrotfish recruits to each site in each of the 2 yr of observation (YR1: April 2003 to March 2004; YR2: April 2004 to March 2005). See Fig. 1 for definition of study sites

between years (Kolmogorov-Smirnov 2-sample test: $p = 0.985$; Fig. 3). The highest numbers of *S. viride* recruits were observed in August/September in YR1 and August of YR2.

Spatial patterns in substrate characteristics and microhabitat selection

Substratum characteristics varied significantly among sites and between null and *Sparisoma viride* quadrats (MANOVA, Sites: Pillai Trace = 1.853; $F_{0.05,65,245} = 2.404$; $p < 0.001$; Quadrat-type: Pillai Trace = 0.669; $F_{0.05,13,44} = 6.854$; $p < 0.001$; Site \times Quadrat-type Interaction: Pillai Trace = 0.782; $F_{0.05,65,240} = 0.685$; $p = 0.964$; Table 2). Sites differed significantly in the percent cover of algal turfs, crustose coralline algae (CCA), *Dictyota* spp., live scleractinian coral, gorgonians, other sessile invertebrates (e.g. sponges and anemones), and in macroalgal height (Fig. 4). Cover of live coral was extremely low at all sites (<4% cover, with the exception of TG, which had 10% coral cover; Fig. 4) and consisted primarily of mounding corals (e.g. *Montastrea* spp.; M. J. Paddack pers. obs.). The patch reefs had significantly lower cover of algal turfs and CCA, higher cover of non-coral sessile invertebrates (sponges), and higher macroalgal height than all other reefs; however, one patch reef (TG) had significantly higher cover of live coral than other reefs (Table 2).

For quadrats with and without *Sparisoma viride*, live coral cover was extremely low and did not differ significantly. Algal turf and CCA cover were significantly higher in null quadrats than in *S. viride* quadrats,

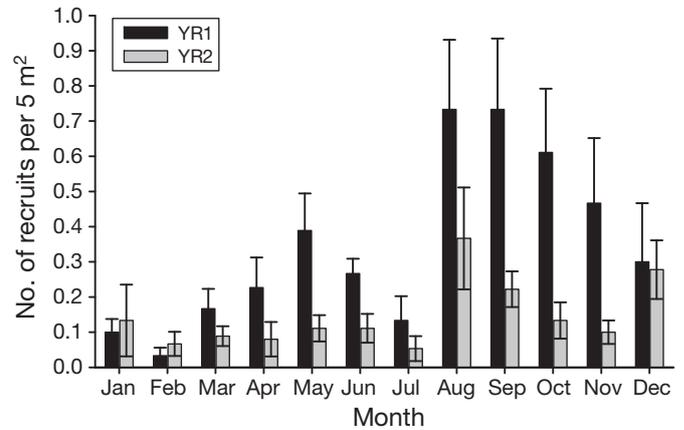


Fig. 3. *Sparisoma viride*. Mean (\pm SE) monthly density of stoplight parrotfish recruits over all sites during each of the 2 yr of observation (YR1: April 2003 to March 2004; YR2: April 2004 to March 2005)

whereas cover of gorgonians and *Dictyota* spp. and macroalgal height were significantly higher in *S. viride* quadrats (Table 2, Fig. 5). *Dictyota* spp. was the most common macroalgae (77 and 78% of total macroalgae in null and *S. viride* quadrats, respectively) and the only group of macroalgae to vary significantly among null and *S. viride* quadrats (Table 2).

Influence of reef characteristics on abundance of *Sparisoma viride* recruits

Of the 3 substratum characteristics that were significantly higher within *Sparisoma viride* quadrats (*Dictyota* spp. cover, gorgonian cover, and macroalgal height), only *Dictyota* spp. resulted in a positive rela-

Table 2. Univariate *F*-test results comparing substratum characteristics among 6 sites in the upper Florida Keys and between quadrats with and without (null) *Sparisoma viride* recruits. Significance indicated by **bold** text. CCA: crustose coralline algae

Source	Sites			Quadrats		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Algal turf	5,56	13.169	<0.001	1,56	38.940	<0.001
CCA	5,56	11.170	<0.001	1,56	16.435	<0.001
<i>Dictyota</i> spp.	5,56	9.773	<0.001	1,56	32.590	<0.001
<i>Halimeda</i> spp.	5,56	2.265	0.060	1,56	2.916	0.093
Other macroalgae	5,56	1.554	0.188	1,56	0.951	0.334
Live stony coral	5,56	6.037	<0.001	1,56	0.015	0.902
<i>Millepora</i> spp.	5,56	1.003	0.425	1,56	0.099	0.754
Gorgonians	5,56	2.654	0.032	1,56	6.727	0.012
Other sessile invertebrates	5,56	3.319	0.011	1,56	2.195	0.144
Macroalgal height	5,56	13.743	<0.001	1,56	7.375	0.009
Turf height	5,56	0.328	0.894	1,56	0.276	0.601
Rugosity	5,56	0.082	0.995	1,56	0.003	0.994

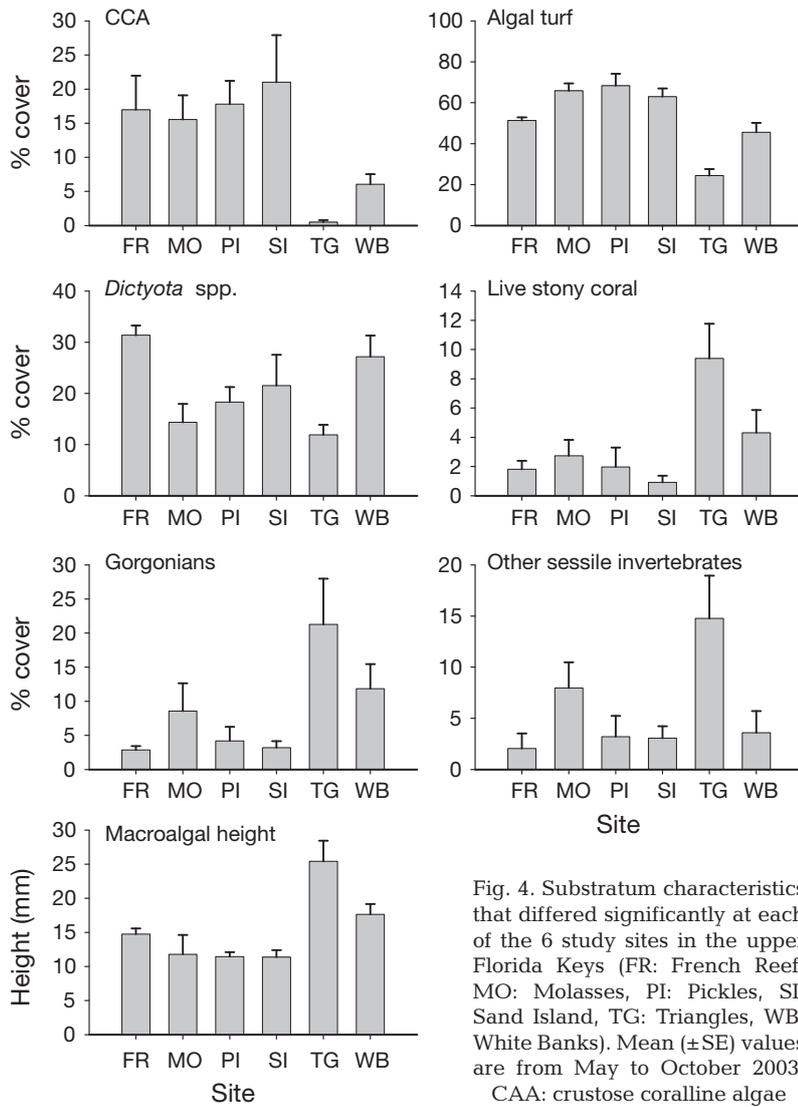


Fig. 4. Substratum characteristics that differed significantly at each of the 6 study sites in the upper Florida Keys (FR: French Reef, MO: Molasses, PI: Pickles, SI: Sand Island, TG: Triangles, WB: White Banks). Mean (\pm SE) values are from May to October 2003. CAA: crustose coralline algae

tionship between percent cover and recruit density among sites. The best-fit relationship between *S. viride* density and *Dictyota* spp. cover at each of the 6 sites was a logistic curve ($y = 0.57 / (1 + 60418.36 \times 1.55^{-1.88x})$, $r^2 = 0.75$, $p < 0.05$; Fig. 6). Recruit density increased at sites with increasing *Dictyota* spp. cover, becoming asymptotic at ~16% *Dictyota* spp. cover.

DISCUSSION

Recruitment of *Sparisoma viride* to the upper Florida Keys, USA, is highly variable over large and small spatial and temporal scales. During our 2 yr study, a high proportion of the spatial variation in recruitment could be explained by the availability of utilized recruitment microhabitat. Our finding that *S. viride* recruits were associated with macroalgal microhabitats diverges

from previous research in the Caribbean which demonstrated selection by *S. viride* for branching live coral (Tolimieri 1998b). Robust recruitment rates of this species to the upper Florida Keys suggest that in the absence of corals, this species can successfully utilize alternative recruitment microhabitat.

High temporal variation in recruitment rates, as we observed for *Sparisoma viride*, is a common characteristic of marine fish populations and is likely driven by a combination of biological and physical factors (Doherty 1991). Inter- and intra-annual variation in recruitment rates of marine fishes and invertebrates have been related to variability in pelagic processes, such as water temperature, currents, and spatio-temporal patterns of phytoplankton blooms (Bergenius et al. 2005, Sponaugle et al. 2006). In the Florida Keys, supply of late-stage fish larvae to reefs is influenced by variations in the position of the Florida Current and the nearshore passage of transient mesoscale eddies (Sponaugle et al. 2005), and the summer peak in recruitment observed for parrotfish reflects overall seasonal patterns in larval supply in the area (D'Alessandro et al. 2007). Late summer peaks in labroid recruitment occur in the Caribbean (Carpenter 1990) despite the fact that *S. viride* spawns daily throughout the year with no evidence of tidal, seasonal, or lunar spawning patterns (Robertson & Warner 1978). The degree to which seasonal cycles of parrotfish recruitment are shaped by physical

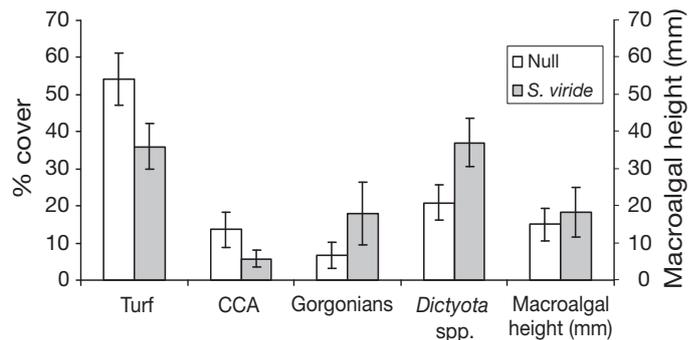


Fig. 5. *Sparisoma viride*. Percent cover (\pm SE) of substrata that varied significantly between quadrats with and without (null) stoplight parrotfish recruits. CCA: crustose coralline algae

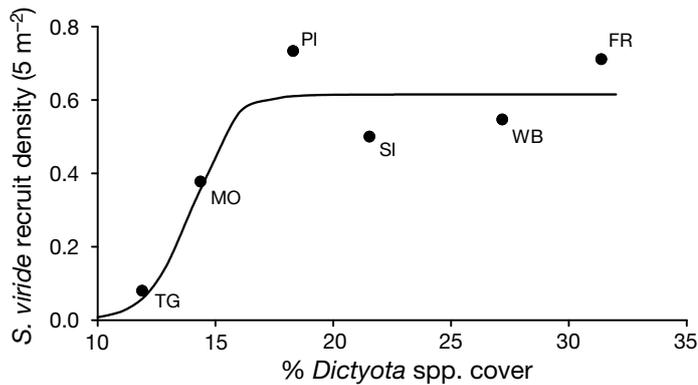


Fig. 6. Relationship of *Sparisoma viride* recruit density to percent cover of *Dictyota* spp. across the 6 study sites (FR: French; MO: Molasses; SI: Sand Island; PI: Pickles; WB: White Banks; TG: Triangles) in the upper Florida Keys. Line is the best-fit relationship as described by a logistic model ($r^2 = 0.75$)

versus biological processes is unknown, but there is some indication that scarid gonadosomatic indices match seasonal patterns of increased food availability (Clifton 1995).

Recruitment rates of *Sparisoma viride* varied spatially among sites in the upper Florida Keys and did not follow any patterns based upon reef type. The inshore patch reefs, in particular, had highly variable densities of recruits: one (WB) had levels similar to the offshore reefs, whereas the other (TG) had very low recruit densities. Given that the supply of settlement-stage larval fishes is generally reduced to inshore reefs (D'Alessandro et al. 2007), the high number of recruits at WB was unexpected. A possible mechanism for such a result is that post-settlement survivorship of scarid recruits is greater at this inshore site than at the other sites. Size frequency distributions of *S. viride* populations on these reefs indicate that inshore reefs have a greater proportion of older juvenile fish, suggesting either that survival is higher inshore or that mortality and/or emigration of adults is more common inshore (Paddack 2005). Cross-shelf differences in scarid abundances and size distributions have been found elsewhere and have been attributed to differential mortality and growth rates (Gust et al. 2001). Although the link between larval supply and recruitment remains poorly understood, the lack of coherence between relative levels of larval supply and recruit density suggests that post-settlement processes occurring within the first few weeks of life vary substantially among reefs and may drive spatial differences in recruitment success. The relative importance of post-settlement processes can be suggested by a lack of a linear relationship between recruit and adult abundance (Doherty 1991); however, we were unable to evaluate this, as to do

so, the study period must span the average generation time of the fish (Holbrook et al. 2000).

Microhabitat differences explained distributions of *Sparisoma viride* recruitment both within and among reefs, as has been shown elsewhere for this species (Tolimieri 1998a). However, a major difference was found in the type of microhabitat selected. In the upper Florida Keys, where total live coral cover is currently extremely low (2 to 10%, Paddack et al. 2006), *S. viride* recruits <20 mm TL predominantly utilized macroalgal microhabitats, particularly patches of *Dictyota* spp. In contrast, *S. viride* recruitment rates in St. Croix, where coral cover was higher (ca. 15 to 40%), were strongly associated with the branching coral *Porites porites* at both small (within reef) and medium (among reefs) spatial scales (Tolimieri 1998b). It was not possible to experimentally compare recruitment preference or impacts upon population dynamics of *S. viride* recruits (e.g. growth and survivorship) in these 2 different microhabitats because *P. porites* and other branching live corals were infrequent in our study area, and *S. viride* recruits in the upper Florida Keys were rarely observed in association with microhabitats other than dense patches of *Dictyota* spp. Without data on the recruitment rates of *S. viride* to the upper Florida Keys prior to the decline in live coral cover, it is impossible to say whether the decline in coral cover and increase in macroalgal cover has positively or negatively influenced the recruitment success of this species or whether microhabitat preferences have changed over time within the Florida Keys. However, recruitment rates of *S. viride* in the upper Florida Keys do not differ greatly from those found in St. Croix (Tolimieri 1998b), and this species remains one of the most abundant herbivorous fishes in the upper Florida Keys (Paddack 2005). These results suggest that *Dictyota* spp. is an effective recruitment substrate when branching corals are unavailable, and the absence of *S. viride* in other microhabitats indicates that *Dictyota* spp. is the only available suitable recruitment substrate for this species in the upper Florida Keys.

The association of *Sparisoma viride* with *Dictyota* spp. may be related to characteristics of the algae that provide resources (e.g. food and shelter) required by newly settled fishes. Coloration and morphology of this alga may be important for shelter, as newly settled *S. viride* have similar coloration and often rest in a 'C' shape, making them extremely difficult to discern within the rounded branch tips of *Dictyota* spp. *Dictyota* spp. are chemically defended by secondary metabolites (Hay & Fenical 1992), and few fishes have been observed foraging in or feeding on patches of *Dictyota* spp. (M. J. Paddack unpubl. data). This may limit interactions of *S. viride* recruits with other fishes within these macroalgal patches, thus reducing preda-

tion risk and competition. *Dictyota* spp. may also provide a source of food for recruits, such as epiphytic algae and micro-invertebrates, upon which scarid recruits feed during the first few weeks of benthic life (Bellwood 1988, Paddack 2005). Other macroalgae do not appear to be utilized by *S. viride* as recruitment microhabitat. Despite the high cover of algae such as *Halimeda* spp. and algal turfs, *S. viride* recruits were rarely found in association with these substrates. Characteristics such as densely packed branches (e.g. *Halimeda* spp.), low structural complexity (e.g. *Lobophora variegata*, algal turfs), or low abundance may limit the suitability of these algae as sufficient refuge for newly settled fishes.

Abundance of *Dictyota* spp. explained a high proportion of the spatial variation in *Sparisoma viride* recruitment at both small (within reef) and large (among reefs) spatial scales. However, on the large scale, this relationship was not linear, but leveled off beyond ~16% *Dictyota* spp. cover. Similar models of non-linear increases to a maximum have been found to describe coral reef fish–microhabitat relationships elsewhere (Wilson et al. 2008), indicating that preferred microhabitat may only substantially influence fish populations when it occurs at low levels. Such a non-linear relationship may also be the result of relatively low regional recruitment rates that prevent further increase in *S. viride* recruit numbers with increasing settlement habitat availability.

Microhabitat selection by recruits has been observed in other tropical reef fish species (Bell & Galzin 1984, Sale et al. 1984), as well as in other ecosystems, including temperate rocky reefs (Andrews & Anderson 2004), kelp forests (Carr 1994), and estuarine and other inshore areas (Levin et al. 1997). However, association of recruits with particular microhabitats is not ubiquitous and may explain little or none of the spatial and temporal variation in recruitment (Tupper & Boutilier 1997, Sale et al. 2005, Wilson et al. 2008). Additionally, the strength of microhabitat associations can vary temporally due to fluctuations in numbers of recruits and/or condition of microhabitat (Carr 1994, Tolimieri 1998b). Thus, our finding that site ranking by recruit abundance was maintained between years and *Sparisoma viride* recruit abundance was positively correlated with the percent cover of the preferred microhabitat, *Dictyota* spp. among sites indicates a particularly strong microhabitat association. Association with specific microhabitats can influence post-settlement survival and growth rates (Levin et al. 1997, Tupper & Boutilier 1997). The costs and benefits of *S. viride* associating with macroalgae rather than branching live coral and the degree to which this association affects later life history stages is unknown. However, the apparent ability of *S. viride* to utilize alternative re-

crutment microhabitats on reefs with depleted coral cover suggests that recruitment of this species may be resilient to changes in benthic reef community structure.

Although factors other than microhabitat can strongly shape recruitment variation over space and time (e.g. reef geography and hydrodynamics; Sale et al. 2005, Sponaugle et al. 2006), our results provide further evidence that small-scale features of the local reef environment can influence the replenishment of reef fish populations. Additionally, in the absence of preferred substrata, some species may be able to successfully utilize other microhabitats. Our finding that *Sparisoma viride* may be able to use macroalgae as recruitment habitat when live coral is not available may have important implications for the resilience of coral reef systems because herbivorous fishes, particularly excavating scarids such as *S. viride*, may be critical to the ecosystem functioning and recovery of coral reefs (Bellwood et al. 2004, Mumby et al. 2006). Such knowledge of the resource requirements of key reef organisms and the degree of plasticity in their use of these resources contributes to our understanding of the factors that influence reef fish demography in changing environments.

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