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Small-scale demographic variability of the biocolor damselfish, *Stegastes partitus*, in the Florida Keys USA

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Abstract The demographic responses of reef fish to their environment can be complex and in many cases, quite strong. Growth, mortality, longevity, and even reproductive effort have been demonstrated to vary for the same species of reef fish over scales of 100s to 1,000s of kilometers due to physiological and ecological interactions. Though few studies have explicitly documented it, this sort of habitat-mediated demography can also exist at very local scales. Here we present the results of a 2-year study of the bicolor damselfish, *Stegastes partitus*, in the Florida Keys, USA. We measured density and distribution, calculated key demographic rates (growth, survival, and fecundity), and characterized the environment (resident fish assemblage, substrate type and complexity, and food availability) of populations living in two adjacent but different habitats, the continuous fore reef and patchy back reef. Fish on the fore reef had an elevated growth rate and asymptotic size, increased mortality, and higher fecundity than fish on the back reef. We identified four potential causative mechanisms for these differences: food availability; competition; intraspecific density-dependent effects; and predation risk. Our data did not support an effect of either food availability or intraspecific density-dependence, but rather suggested that demographic responses are affected by both competition and predation risk.

Keywords Fecundity · Growth · Survival · Coral reef fish · Habitat · Plasticity

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Introduction

An ever increasing body of research on tropical reef fishes has demonstrated substantial spatial variability in demographic rates over quite large spatial scales (e.g., Kritzer 2002; Williams et al.

2003). In many instances consistent patterns of variability occur in concert with changes in latitude (Choat et al. 2003; Robertson et al. 2005). In addition to the positive size-latitude relationship that would be predicted for ectotherms in general (Atkinson and Sibly 1997), fish at higher latitudes also tend to live longer and have lower rates of mortality than fish at lower latitudes (e.g., Choat et al. 2003; Robertson et al. 2005). These differences have been attributed to predation (Meekan et al. 2001), fishing pressure (Choat et al. 2003), ocean productivity (Williams et al. 2003) and temperature-mediated tradeoffs between longevity and reproduction (Robertson et al. 2005). Demographic variability has also been demonstrated at smaller scales. Ruttenberg et al. (2005) saw trends in the mortality and maximum size and age of the damselfish, *Stegastes beebei*, at clustered Galapagos Island sites (<150 km apart) and attributed the differences to variability in food availability and reproductive energy allocation at cold versus warm water sites. Cross-shelf gradients in growth, mortality, and longevity of other reef fish over distances as small as 20 km have been attributed to turbidity (Kritzer 2002) and density-dependent processes (Gust et al. 2002; Gust 2004).

These studies demonstrate a variety of mechanisms that may account for observed demographic variability. At vary large scales, physiological constraints are likely to affect energy allocation and play a dominant role in driving the observed patterns. However at smaller scales, variability very likely results from the often plastic response of reef fish to many components of their environment. Local demographics will be most affected by factors such as food availability, inter-specific competition, intra-specific density-dependence and predation. Studies have demonstrated the effect of food availability on growth (Jones 1986), survival (Nemeth 1997), and even courtship intensity (Knapp 1995) of fish. Density-dependent processes such as inter-specific competition can also strongly affect resource allocation and therefore growth, survival, and reproduction (Nemeth 1997; Levin et al. 2000). Intra-specific density-dependent processes can also play a role. These

could be in the form of competition for mates, breeding territories, or refuge from predation (e.g., Warner 1991; Holbrook et al. 2000; Gust et al. 2002). Lastly, predation pressure can be a very powerful force structuring reef fish communities (reviewed in Hixon and Jones 2005) and thereby influence individual demographic rates and life history strategies (Stearns 1992).

It is likely that demographic variability exists over very small spatial scales (10s of kilometers), however relatively few studies have documented such patterns. There is some evidence that mortality and survival do vary at these spatial scales for several species of reef damselfish (e.g., Nemeth 1998; Levin et al. 2000) yet few studies have thoroughly documented multiple demographic components in concert with complete habitat characterization in order to assess support for the various potential causative mechanisms described above. In this paper, we present the results of a 2-year study of the abundance, distribution, growth, survival, and fecundity of the biocolor damselfish, *S. partitus*, in two very different habitats. The fore and back reef zones of the southern Florida Keys reef system are only about 2.5 km apart and thus have many species of fish in common, but they differ structurally. The fore reef is an approximately 750 m wide continuous strip of habitat consisting of predominately hard corals and rock. On the back reef side, however, is Hawk channel, which contains large isolated patches of coral/rock reefs surrounded by sand and/or seagrass. In contrast to the relatively open structure of the continuous fore reef zone, soft and branching corals create a canopy of structure across most of the patch reefs that dominate this back reef/mid-channel zone. In addition to quantifying the demographic rates of fish in each of these reef zones, we also characterized the habitat to quantify the physical and biotic differences between the two reef types. We synthesize this information to document demographic variability and to determine which of the four causative mechanisms discussed above (food availability, intra-specific density-dependent effects, inter-specific competition, and predation pressure) is most likely responsible for this variability.

Materials and methods

Study organism

Stegastes partitus is a highly site-attached, territorial, planktivorous Pomacentrid found on reefs throughout the Caribbean Sea. Individuals generally settle and remain on the same coral head for the duration of their lives (McGehee 1995). Spawning occurs on a lunar cycle beginning a few days before the full moon and ending a few days after the new moon. During the first 60–90 min after dawn, females will enter male territories and lay down a discrete monolayer of eggs in a nest maintained by the male. Males are sequentially polygynous and nests therefore often contain clutches of eggs from different females in various stages of development (eggs take 3.5 days to hatch), which can be differentiated by their color (Schmale 1981).

Site demarcation and mapping

Our research sites were located just outside the western border of the Western Sambos Ecological Reserve, Florida Keys National Marine Sanctuary, USA. We established (randomly) five permanent 15 m × 15 m sites of similar depth (~8 m), three in the continuous habitat near the reef crest (fore reef) and two about 2.5 km landward on a large isolated patch reef in Hawk channel (back reef). Establishment of a third back reef site was prevented by Hurricane Irene in September 1999. Site boundaries (in the cardinal directions) and six permanent transects (three in the N–S direction and three in the E–W direction), were demarked using rope and corner stakes. Using these lines as a reference, the site was mapped by drawing onto a dive slate the approximate location and size of all coral heads or other topographic features that might serve as refuge for *S. partitus*. These areas, which we termed "high rugosity areas" (HRAs), are topographically complex portions of the habitat upon which fish are typically found, apparently due to the relief they offer or the refuges they supply. Between September 1999 and September 2001 we made four visits to the sites: September 1999 (4 weeks); May–June 2000 (6 weeks); June 2001 (3 weeks); and August–September 2001 (4 weeks).

Note on statistical analyses

Data collected during this study characterized: (1) the abundance and distribution of resident *S. partitus*, (2) the habitat in which these fish live, and (3) their demographic rates. We make frequent use of one-way, nested and repeated measures ANOVA (RM-ANOVA) to test for differences between reef zones (back vs. fore reef) in our data analysis. In all cases data were examined for normality, tested with Cochran's test for homogeneity of variance and Mauchley's test for sphericity (where necessary with RM-ANOVA). When needed, data were transformed or an equivalent non-parametric test was used. For the sake of brevity, we mention only instances where such alterations were required.

Fish distribution and abundance

We conducted two different censuses to quantify the abundance as well as the distribution of *S. partitus* at each site: "standard" and "spatial". When conducting a standard census, a diver slowly swam over the entire site using transect lines for reference and noted the total length (using a "T"-bar for reference), to the nearest 5 mm, of every *S. partitus*. For the spatial census, the location of each fish was mapped and instead of exact sizes, fishes were grouped into size categories by total length: recruit (≤25 mm); juvenile (>25 and ≤50 mm); or adult (>50 mm). Five standard censuses of all sites were conducted over the course of the study. Spatial censuses, however, were only conducted once during each of the two 2001 visits. Standard census data were assigned to size categories as described above for the spatial censuses. We used RM-ANOVA to test differences in overall densities of each size class between reef zones for all five sample periods. Spatial census data were used to further explore the distribution of *S. partitus*. The data sheets from the spatial censuses were scanned and on-screen digitized as georectified point theme

layers in ArcView (version 3.2, ESRI). We used this data to calculate an aggregation index *R* (Clark and Evans 1954) as well as the average nearest neighbor distance for each site at each of the two spatial censuses. Comparisons were made between reef zones using a RM-ANOVA.

Due to the patchy distribution of this species within a site, the relevant density estimate may not be at the scale of the entire site but rather at the local scale of the aggregations in which these fish occur. To account for this, we calculated an ''effective'' density for each site at each of the two spatial censuses. We divided the sites into 1 m quadrats in our ArcView coverages and then calculated the average density using only those quadrats where fish occurred. We again used RM-ANOVA on site averages to compare between reef zones for both spatial censuses.

Habitat: site-level reef zone comparisons

We measured rugosity (the ratio of the straight-line length along a transect to the length following the contours of the surface, Luckhurst and Luckhurst 1978) along each of the six transect lines in each site at the beginning of the study (yielding 6 points per site) and compared values between reef zones using a nested ANOVA (sites within reef zone). Percent cover was measured using uniform point sampling (0.25 m^2 quadrat) at three random points along each of the six transect lines (giving 18 samples per site). We characterized sites within reef zones using Principle Component Analysis and tested for statistical differences between zones for each cover type using a nested ANOVA (sites within reef zone) on ranked data (as assumptions were not met) following the methods of Quinn and Keough (2002).

We characterized fish assemblages at each site once in 1999 and twice in 2001 by conducting visual censuses (2 m swath size) on the three 15 m site transect lines aligned most parallel with the direction of the current (to facilitate maintaining of position). Censused fish species were grouped into ecologically relevant categories; Predators (classified following Nemeth 1998), Serranids (because they were very common), Competitors

(fish commonly observed in agonistic interactions with *S. partitus*), other Pomacentrids (subset of competitors), and Labrids (very common egg predators). Between-reef zone comparisons were made for each group with nested (sites within reef zone) RM-ANOVA.

Behavioral observations of *S. partitus* in both reef zones during different times of day indicated both juvenile and adult sized fish consistently had very low levels of benthic compared to planktivorous feeding (bites per 10 min ± SE: benthic = $1.2 ± 0.19$, planktonic = $16.0 ± 2.2$, Lyman unpublished data) and thus we followed the methods of Nemeth (1997, for this same species) and estimated food availability as the amount of planktonic copepods in the water column. This was done by deploying passive collection tube traps (5.1 cm diameter and 60 cm tall, containing 10% buffered formaldehyde, Yund et al. 1991) for 2 weeks (during fecundity monitoring) in 2000 (4 traps per site) and 2001 (3 traps per site). We processed samples by filtering them through a 63 μm mesh sieve, staining with rose bengal and enumerating copepods, [the primary prey item of *S. partitus*, Nemeth (1997)] under a dissecting microscope. We used nested (sites within reef zone) ANOVAs to compare the total number of copepods collected per hour between reef zones.

Habitat: HRA-level measurements

High rugosity areas identified as territories for *S. partitus* during the demographic studies (described below) were marked with semi-permanent tags attached to non-living substrate. We estimated the volume of each HRA by assuming that it was a domed elliptical cylinder. Rugosity was estimated by measuring along transects running in each of the cardinal directions over the highest point of the HRA. We estimated hole density and area by counting and measuring all holes that fell within 5 cm of either side of each of the two transects used for rugosity (Friedlander and Parrish 1998; Nemeth 1998). A single diver slowly swimming around the HRA characterized resident fish assemblages (species and size) and estimated percent cover (nearest 5%).

Demographic: growth and survival analyses

We used a mark-recapture design to estimate growth and survival over the course of the 2-year study. We captured fish (noting location on map) using hand nets and a 2% quinaldine solution, then transferred them to plastic bags where we measured and uniquely marked each fish with subcutaneous fluorescent elastomer tags (Northwest Marine Technology, Inc.) that are commonly used for reef fish, including *S. partitus*. These tags are well retained and have no significant effect on mortality or growth rate (Beukers et al. 1995; Frederick 1997). Fish were captured or recaptured on five occasions, September 1999, May 2000, June 2000, June 2001, and August 2001 (termed bouts 1–5 respectively). During each bout after the initial one, all fish within the site plus 3 m from the perimeter were carefully inspected for marks. We captured and measured marked fish and noted any change in territory location. Unmarked fish were measured, marked, and mapped so as to be included as new marks-at-large for the next return visit.

Growth analysis

We used the von Bertalanffy growth interval equation, $L_2 = L_\infty - e^{k\Delta t}(L_\infty - L_1)$, where L_1 and L_2 are the length of the fish at the beginning and end of the interval whose length is Δt (Quinn and Deriso 1999), and estimated the growth (k) and asymptotic size (L_∞) parameters by fitting data on fish total length using the non-linear estimation module of Statistica (version 6.0) with a least squares loss function. Separate equations were fit for each site. Due to low sample sizes, we combined data from bouts 1–4 making sure that no individual fish was represented in more than one bout (for independence of data). We then fit curves by site to bout intervals 1–4 and 4–5 separately. Of the ten resulting growth curve estimates (four on the back reef and six on the fore reef) for each of the two parameters, we selected only those with significant fits ($P < 0.05$) and adequate sample sizes ($n > 5$) and compared average values for each reef zone on a k versus L_∞ plot with 95% confidence intervals indicated (Kimura 1980).

Survival analysis

Survival rates were calculated for each site over each bout by dividing recaptures by the number initially marked; assuming that fish were dead if not found within the site plus the 3 m buffer zone we searched around it. The exhaustive search required to calculate survival rates was not performed during bout 3 (June 2000, as described above), so bouts 2 and 3 are combined for the survival analysis (and called ''bout 2/3''), leaving three intervals over which we could estimate survival: 1–2/3, 2/3–4 and 4–5. As the three bouts were not of equal length we calculated an instantaneous mortality rate (z) for each site over each interval (McGehee 1995) and compared the rates between reef zones using RM-ANOVA. We then adjusted these estimates to account for any emigration that may have occurred using Jackson's (1939) square within a square technique [see Etherington et al. (2003) for an example of this applied to benthic marine organisms]. This technique sub-divides the square study area into four smaller squares and relies on the premise that the emigration rate from the squares, small and large, will be proportional to their perimeter to area ratio. Unfortunately only bout 4–5 had a high enough sample size to apply Jackson's (1939) technique. We used the resulting site-specific corrections (corrected divided by uncorrected value) for this bout to correct estimates for each site from all other bouts. As these are extrapolations, however, we did not apply any statistical tests and rely on the results of the RM-ANOVA of uncorrected mortality as an indication of reef zone differences.

Demographic: fecundity monitoring

Ten actively courting males at each site were provided with 13 cm diameter clay flowerpots (stabilized with 0.9 kg dive weights) as spawning substrate in June of 2000 and August–September of 2001. This artificial spawning substrate controls for nest quality, makes monitoring of nests easy, and is readily used within a few days by males (e.g., Knapp et al. 1995). After a 3 week acclimation period, nests were visited every 3rd day for a 2 week period around peak spawning and the

outline of all clutches was traced onto acetate sheets, noting the color of each clutch to estimate its age (Schmale 1981). We scanned tracings, determined the area of each clutch with MOCHA image analysis software (Jandel Inc.) and estimated the total number of clutches and area of eggs received over each monitoring period for each male. We controlled for any effects of the time of onset of spawning (back reef fish seem to start a few days later in the lunar cycle) by normalizing area received by the number of days since first spawning. To address the potential effect of mate encounter rate, we normalized total area received by the number of clutches. Reef zone and year differences for site averages of all three variables (clutch, area received/clutch, and area received/day since first spawning) were tested with RM-ANOVA.

Demographic-habitat comparison

We examined relationships between the measured habitat variables and our estimated demographic responses (growth, fecundity and survival) at the scale of individual HRAs using single and multiple regressions. Growth rates (k) for individual fish were estimated from the von Bertalanffy equation by assuming an asymptotic size (L_∞) for each fish equal to that determined for that fish's site in the growth analyses (described above). Growth data (excluding fish which were not growing much, TL > 55 mm) were regressed (simple linear) against each of the HRA-level measurements for the HRA on which that fish was found. Fecundity data (number of clutches, total area of eggs received per clutch, and total area of eggs received per day since first spawning) for individual fish were analyzed in a similar manner but there was no restriction on the size of fish used as long as they had received at least one clutch during the monitoring period. The effect of each HRA-level variable on survival was assessed using logit regressions where the state of each fish in the study at the end of an interval (alive or dead) was regressed against each characteristic of that fish's resident HRA. Based on these regressions, we picked the most influential (significant) variables for inclusion in multivariate regressions against

each demographic variable with the goal of determining the best-fit model to establish the relative importance of each.

Results

Distribution and abundance

Over the course of the 2 year study the standard density of all size classes of *S. partitus* increased significantly—by about fourfold—at each site (RM-ANOVA census effect *P*-values for all size classes <0.003). While fish density was higher on the fore reef for all size classes (individually as well as combined) the differences were only significant for recruits ($P = 0.011$), juveniles ($P = 0.005$), and all sizes combined ($P = 0.043$, Fig. 1a).

The Clark and Evans (1954) R-aggregation analysis of the spatial census data showed that with only one exception, fish were distributed randomly on the fore reef and clumped on the back reef. The distance to the nearest neighbor was slightly greater on the back reef ($P = 0.023$; back reef: mean ± SD = 0.90 ± 0.10 m, $n = 4$; fore reef: mean ± SD = 0.80 ± 0.13 m, $n = 6$)
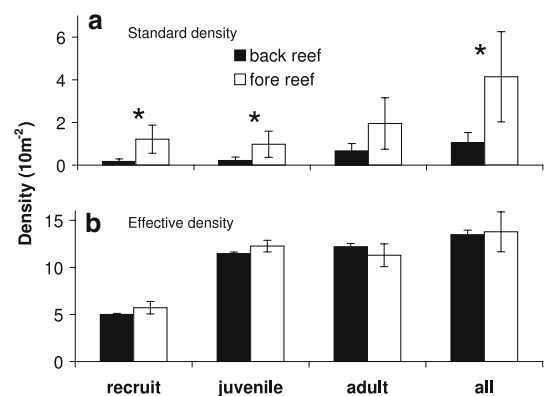

Fig. 1 Average (±SD)''standard'' (**a**) and ''effective'' (**b**) density of *S. partitus* in each reef zone from all censuses. Size classes were based on total length: ≤25 mm—recruit; >25 mm but ≤50 mm—juvenile; >50 mm—adult. ''*'' indicates significant differences between reef zones from repeated measures ANOVA of data from all census bouts. Sample sizes were 10 and 15 (back and fore reef respectively) for the standard and 4 and 6 for the effective density analyses

however this small distance of only 10 cm is unlikely of any biological significance and falls well under our mapping error of approximately 0.5 m. There was no significant difference in effective density between the two reef zones (Fig. 1b).

Habitat: site level reef zone comparisons

Overall the back reef sites were significantly more rugose than the fore reef sites (back reef: mean ± SD = 1.51 ± 0.34, n = 18; fore reef: mean ± SD = 1.30 ± 0.30, n = 12; nested ANOVA habitat P-value << 0.001). PCA analyses of percent cover data indicated that the first two factors accounted for 64.5 and 17.6% of the total variation. Back and fore reef sites separated strongly along factor 1 (Fig. 2a) which was loaded positively by sand and rubble (fore reef sites) and negatively by branching and massive corals (live and dead) and fan coral (back reef sites, Fig. 2b). Nested ANOVAs on ranked data indicated that all of these habitat differences were significant (P < 0.008) except for rock (P = 0.238).

The nested RM-ANOVAs on site level fish census data (Table 1) indicated that the only strong differences between reef zones was Labrids which were more dense on the fore reef (reef zone P < 0.001) and other Pomacentrids which were less dense there (reef zone P = 0.002). The number of copepods collected in plankton traps was not significantly different between reef zones for either the 2000 (mean ± SD: back reef = 5.62 ± 3.4, n = 7; fore reef = 4.18 ± 2.09, n = 10, reef zone P-value = 0.146) or the 2001 deployment (mean ± SD: back reef: = 3.42 ± 1.21, n = 6; fore reef = 3.34 ± 1.22, n = 9; reef zone P-value = 0.893).

Demographic: growth

Sample sizes for the growth model fits to each site for bout 1–4 were 10 and 12 for the two back reef sites and 3, 10, and 5 for the three fore reef sites. For bout 4–5, sample sizes were 26 and 36 for the back reef sites and 34, 28, and
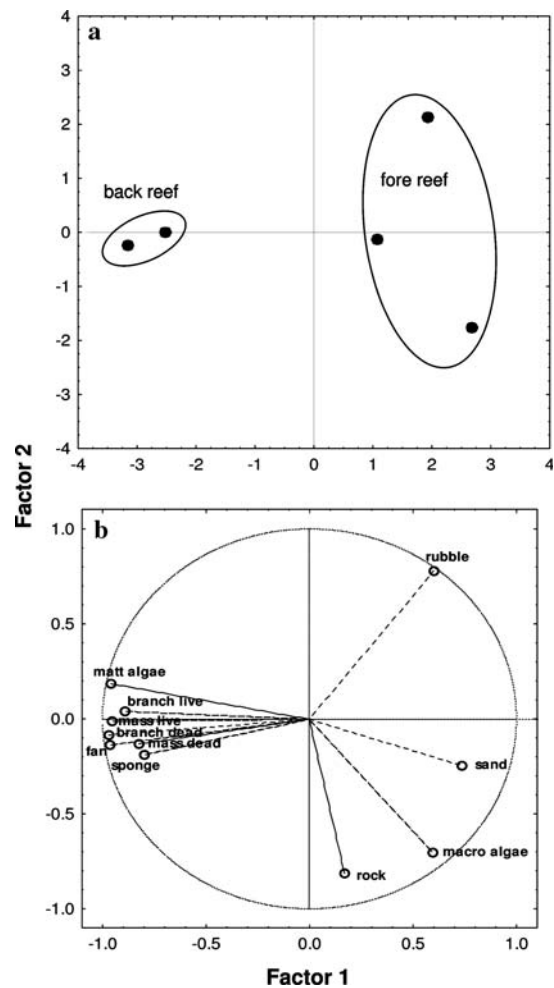

Fig. 2 Projection of cases (**a**) and variables (**b**) on the first two factors from the principle component analysis of site-level percent cover data (square-root arcsine transformed). The variance explained was 64.5 and 17.6% for factors 1 and 2 respectively. Nested ANOVAs on ranked data (see text for details) indicated all variables were significantly different between the two reef zones except rock

13 for the fore reef sites. Model fits to the data generated a total of nine significant parameter fits for asymptotic size (4 back reef and 5 fore reef) and seven significant fits for growth rate (4 back reef and 3 fore reef). Visual comparisons of two-dimensional 95% confidence intervals indicated that both asymptotic size [L_∞ (mm), fore reef = 72.7, back reef = 67.3] as well as growth rate [k (days^{-1}), fore reef = 0.0075, back reef = 0.0056] were greater on fore reef than on back reef sites (Fig. 3).

Table 1 Average density of fish in each interaction category in fore reef (FR) and back reef (BR) zones during each of the three censuses (one in 1999 and two in 2001)

| | Density (fish 10 m^{-2}) | | | | | | Nested RM-ANOVA | | |
| | 1999 | | 2001a | | 2001b | | P-values | | |
	BR	FR	BR	FR	BR	FR	Zone	Census	Zn^{a}Cen
Resident predators	0.4	0.0	0.3	0.1	0.4	0.3	0.093	0.372	0.600
Transient predators	0.2	0.6	0.0	0.0	1.7	0.0	0.208	0.121	**0.024**
Serranidae	0.4	0.2	0.3	0.3	0.4	0.4	0.397	0.612	0.693
All predators	0.6	0.6	0.3	0.1	2.2	0.3	0.059	**0.047**	**0.032**
Competitor	13.9	9.1	10.6	11.5	13.7	16.9	0.936	0.142	0.232
Other pomacentridae^a	2.6	0.5	1.0	0.4	1.5	0.6	**0.002**	**0.012**	**0.014**
Labridae^b	2.1	5.7	1.6	7.8	3.4	10.0	**0.000**	**0.015**	0.233

P-values are for effects of reef zone, census, and their interaction as determined by nested repeated measures ANOVA tests. There were no significant values for the nested effect (sites within habitat, all $P > 0.07$) and thus they are not listed. For each census $n_{back\ reef} = 6$, $n_{fore\ reef} = 9$ (three replicate transects per site per census). Significant P-values are shown in bold

[a] Members of this group are also included in "Competitor" group

[b] Members of this group are also variously included in the "Resident" and "Transient predator" categories depending on species

Demographic: survival

We marked a total of 377 fish in all sites over the 2 years of the study. Over this period mortality was about 2.8 times higher on the fore reef sites than on the back reef sites (RM-ANOVA habitat P-value = 0.021). The application of Jackson's (1939) technique indicated very low levels of emigration and corrected mortality estimates were still 2.4 times greater on the fore reef (Table 2).
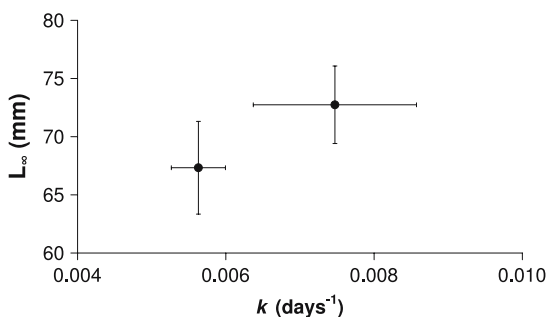
Demographic: fecundity

Fore reef fish received a significantly greater area of eggs per spawning day than did back reef fish (RM-ANOVA reef zone P-value = 0.017) and overall fecundity during the monitored cycle was greater during 2000 than 2001 (RM-ANOVA Year P-value = 0.002, Fig. 4). Analysis of the other measures of fecundity indicated that this was not simply because of the difference in the number of clutches received (RM-ANOVA on number of

Fig. 3 Average (with 95% CI) von Bertalanffy growth parameters for *S. partitus* in the fore and back reef zones. Parameters are averages of estimates derived from significant growth model fits to data from each site and bout (1–4 and 4–5 separately (as described in text). Back reef growth constant (k) was 0.0056 days^{-1} and asymptotic size (L_∞) was 67.3 mm. Fore reef growth constant (k) was 0.0075 days^{-1} and asymptotic size (L_∞) was 72.7 mm

Table 2 Original and movement corrected mortality estimates [z-values (day^{-1})] and corresponding monthly survivorship for *S. partitus* in each reef zone

	BR	FR	P-value
Original mortality	0.0032	0.0091	0.021
Corrected mortality	0.0034	0.0083	
Monthly survivorship	0.903	0.777	

Original mortality values calculated from averages for all sites in each habitat over all three sample bout intervals (1–2/3, 2/3–4, and 4–5; see text for details). P-value indicates significance of difference between reef zones based on repeated measures ANOVA ($n_{back\ reef} = 6$, $n_{fore\ reef} = 9$). Statistical comparison not possible on corrected values (see text for details). Monthly survivorship values were calculated assuming exponential mortality for 30.4 days
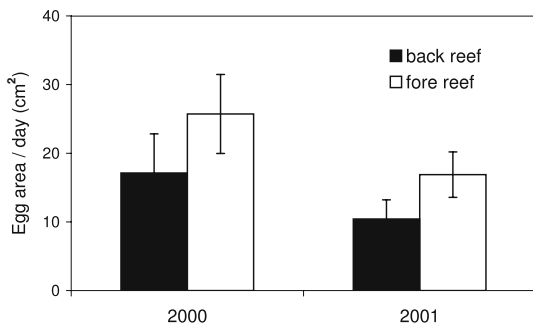
Fig. 4 Average (±SE) area of eggs received per day spawning by males on fore and back reef sites during the 2000 and 2001 monitoring periods. Repeated measures ANOVA on site averages indicated a significant effect of reef zone ($P = 0.017$) and also of year ($P = 0.002$) but no interaction. Sample sizes used to calculate site means were 3, 6, 5, 7, and 8 in 2000 and 7, 7, 9, 9, 8 in 2001 for the two back reef and three fore reef sites respectively

clutches, reef zone P-value = 0.067) but rather was at least partly related to larger clutch sizes on the fore reef (RM-ANOVA on area/clutch, reef zone P-value = 0.021).

HRA-level habitat-demographic relationships

As all three fecundity measures were highly correlated, the results for each were very similar and thus we present only those based on total area of eggs received per spawning day. Single variable regressions of demographic data against HRA-level characteristics generated some very common trends (Table 3). Of the resident fish assemblages, there was no effect of *S. partitus* density on either growth ($P = 0.430$), fecundity ($P = 0.378$), or survival (0.529). The density of other Pomacentrids and competitors was negatively related to growth ($P = 0.050$ for both) and fecundity ($P = 0.012$ and 0.007 respectively) but not to survival ($P = 0.094$ for both). Predators were observed so infrequently that their effect could not be tested. Of the variables describing complexity and size (rugosity, volume and surface area), only the negative relationship between rugosity and growth was significant ($P = 0.051$). The density of holes <25 cm^2 and

Table 3 Summary of regression tests relating habitat variables to *S. partitus* growth (k), fecundity (area/day spawning), and survivorship at the scale of individual HRAs

HRA variable	Growth [k (day^{-1})]			Fecundity (area spawning day^{-1})			Survival	
	r^2	Slope	P	r^2	Slope	P	Estimate	P
S. partitus density (m^{-2})	0.053	–0.00052	0.430	0.017	0.658	0.378	0.136	0.529
Predator density (m^{-2})	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Competitor density (m^{-2})	**0.283**	**–0.00079**	**0.050**	**0.146**	**–3.612**	**0.007**	0.534	0.094
Other Pom. density (m^{-2})	**0.283**	**–0.00079**	**0.050**	**0.128**	**–3.410**	**0.012**	0.534	0.094
Rugosity	0.283	–0.00438	0.051	0.049	–10.031	0.125	1.866	0.103
Volume (m^3)	0.126	0.01196	0.214	0.004	3.072	0.664	0.195	0.889
Surface area (m^2)	0.073	0.00135	0.350	0.004	0.643	0.685	–0.016	0.954
Density (m^{-2}) holes: <25 cm^2	**0.428**	**–0.00003**	**0.011**	**0.132**	**–0.048**	**0.010**	**0.029**	**0.003**
Density (m^{-2}) holes: 25–50 cm^2	0.140	–0.00012	0.187	0.001	–0.030	0.836	0.041	0.189
Density (m^{-2}) holes: 50–150 cm^2	0.001	–0.00001	0.906	0.000	0.013	0.947	0.025	0.432
Density (m^{-2}) holes: >150 cm^2	0.008	0.00006	0.757	0.037	–0.515	0.187	–0.111	0.120
Density (m^{-2}) holes: all	**0.450**	**–0.00003**	**0.009**	**0.143**	**–0.051**	**0.007**	**0.029**	**0.002**
Massive coral (%)	**0.317**	**0.00003**	**0.036**	**0.136**	**0.089**	**0.009**	–0.015	0.078
Branching coral (%)	**0.431**	**–0.00004**	**0.011**	**0.154**	**–0.106**	**0.005**	**0.036**	**0.014**
Fan coral (%)	n/a	n/a	n/a	0.041	1.348	0.165	3.531	0.996
Sponge (%)	0.001	–0.00001	0.909	0.003	–0.027	0.724	–0.013	0.317
Sand (%)	0.083	0.00006	0.319	0.003	0.071	0.727	–0.034	0.279
Algae (%)	0.029	–0.00001	0.561	0.001	0.011	0.850	0.003	0.761

Growth and fecundity results are from simple linear regressions of data from all sample bouts. Growth rates (k) were calculated for individual fish as described in the text. Survival results are from logit regressions on the probability (1 or 0) of an individual fish surviving from sampling bout 4 to bout 5 (to allow for maximal sample size). For all results, the sign of the slope indicates the direction of the relationship while r^2 (not available for logit regressions) and P indicate respectively, the variance explained by and the significance of the regression coefficient. P-values ≤ 0.05 are indicated in bold text. Sample sizes were 14, 49, and 85 for growth, fecundity and survival respectively

of all holes combined were both negatively correlated with growth ($P = 0.011$ and $P = 0.009$ respectively) and fecundity ($P = 0.010$ and $P = 0.007$ respectively) and positively with survival ($P = 0.003$ and $P = 0.002$ respectively). The only significant effects of the cover types were for the percent cover of massive and branching coral. Branching coral was negatively related to growth ($P = 0.011$) and fecundity ($P = 0.005$) and positively related to survival ($P = 0.014$) while massive coral was the exact opposite ($P_{growth} = 0.036$, $P_{fecundity} = 0.009$) though the relationship to survival was not significant ($P = 0.078$).

Based on these univariate regressions we selected five variables for the best-fit model regressions: competitor density (m^{-2}), rugosity, density of all holes (m^{-2}), percent cover of massive coral, and percent cover of branching coral. The best-fit model for fecundity explained only 22% of the variability and included only the percent cover of branching coral ($P = 0.041$) and the density of competitors ($P = 0.052$), both of which were negatively related to fecundity (Table 4). The model for growth explained 55% of the variability and again included these two variables as negative factors ($P_{branching} = 0.048$, $P_{competitors} = 0.222$) though the latter coefficient was not significant. The best-fit model for survival based on Akaike Information Criteria included only the negative effect of the density of all holes ($P = 0.049$).

Discussion

Our study demonstrates demographic variability of *S. partitus* inhabiting two adjacent but structurally different reef zones and supports the idea that this arises due to plastic demographic responses to the local habitat. Fish living on the less structurally complex fore reef grew faster and larger, and had higher per capita fecundity, but had much lower survival. As this is a size-based study we did not obtain estimates of longevity. Given the latitudinal trends observed by Caldow and Wellington (2003), however, we might expect Florida Keys populations to have longevities somewhere between the 2–3 years reported for Puerto Rico (McGehee 1995) and the 7 years reported for the northern Gulf of Mexico (Caldow and Wellington 2003). In fact, several back reef fish were present for the duration of the project (2 years) and based upon calculated growth trajectories, these fish were already close to 2 years old at the time of marking. The same was not true of the fore reef fish with few if any fish caught in more than one recapture bout. Thus while not estimated specifically in this study, back reef fish longevities of 4+ years do seem to correspond roughly with that expected based upon age-based studies of *S. partitus*. However, those for fore reef fish are likely to be much lower than expected (1–2 years).

The larger asymptotic size of fore reef fish suggests that the higher per capita male fecundity

Table 4 Results of multiple regressions indicating the best-fit models relating fecundity (area/clutch), growth rate (k), and survival to the five key HRA-level variables (as discussed in text): competitor density (m^{-2}), rugosity, density of all holes (m^{-2}), percent cover of massive coral, and percent cover of branching coral

Demographic variable	Best model variables	Estimate	*P*-value
Fecundity $r^2 = 0.22$, , $P = 0.004$	Branching coral (%) Competitor density (m^{-2})	–0.293 –0.278	0.041 0.052
Growth $r^2 = 0.55$, , $P = 0.038$	Branching coral (%) Competitor density (m^{-2})	–0.524 –0.304	0.048 0.222
Survival AIC = 99.66, $P < 0.001$	Density (m^{-2}) holes: all	0.023	0.049

Fecundity and growth models resulted from backwards stepwise multiple linear regressions. The survival model represents the best-fit [of all possible subsets based on Akaike information criteria (AIK)] from a multiple logit regression. The overall quality of the fit is indicated by the r^2 and *P*-values for the linear regressions and the AIC- and *P*-values for the logit regression. Sample sizes were 14, 49, and 85 for growth, fecundity and survival respectively

could simply be the result of larger females. Analysis of the tagged fish data indicates that the average size of adults (>50 mm TL) was 61 mm on the back reef and 64 mm on the fore reef. Assuming fecundity scales with the cube of body size (Moyle and Chech 2003) we can generate predicted fore reef fecundity (total area received) based on the observed back reef fecundity for both the 2000 and 2001 measurement periods. These calculations indicate that this predicted fore reef fecundity is only 54 and 33% of the observed fore reef fecundity in 2000 and 2001 respectively. Thus, while somewhat larger females on the fore reef might play some role, size distribution alone cannot account for the entire difference in fecundity.

Causative mechanisms

Our analyses suggest that multiple environmental variables are interacting to generate the observed demographic differences and no single mechanism (as outlined previously) fully explains the difference (summarized in Table 5). In Table 5 we list the four mechanisms along with variables measured in this study that relate to each. We have summarized the findings of this study for the reef zone level comparisons (Fore reef relative to back reef, group A) and the HRA-level regressions (group B). We evaluate the role of each mechanism in three ways. First, we note that each of the potential causative mechanisms (food availability, intraspecific density dependence, inter-specific competition, and predation risk) has specific predictions (in most cases) as to the effect on each of the three demographic variables measured in this study (Table 5, group C). Comparisons of the regression modeling results (Table 5, group B) with these predictions indicate the support (bold arrows in Table 5, group C) or lack thereof for each mechanism. Secondly, we can generate expectations as to the relative strength (fore reef relative to back reef)

Table 5 Summary of observed reef zone comparisons ("Group A") and HRA-level regression results ("Group B") from this study along with comparisons to expected results for each of the proposed causative mechanisms

Mechanism	Variable	Observed				Expected					
		Group A	Group B			Group C			Group D		
		FR relative to BR	HRA-regression			HRA-regression			FR relative to BR		
			G	F	S	G	F	S	G	F	S
Food	Copepod abundance	↔	n/a	n/a	n/a	⇑	⇑	⇑	⇑	⇑	⇓
Competition	Competitor density	⇓	⇓	⇓ᵃ	↑↑	**⇓**	**⇓**	⇓	**⇓**	**⇓**	⇑
Density-dependent	Distance/spacing	↔	↔	↔	↔	⇓	⇑⇓	⇓	⇓	⇑⇓	⇑
Predation risk	Predator density	↔	↔	↔	↔	⇓	⇓	⇓	⇓	⇓	⇑
	Site rugosity	⇓	n/a	n/a	n/a	⇑	⇑	⇑	⇑	⇑	⇓
	HRA rugosity	↓	⇓	↔	↑↑	⇑	⇑	**⇑**	⇑	⇑	⇓
	HRA size	⇑	↔	↔	↔	⇑	⇑	⇑⇓	**⇑**	**⇑**	**⇑⇓**
	HRA hole density	⇓	⇓	⇓	⇑ᵃ	⇑	⇑	**⇑**	⇑	⇑	⇓
	Massive coral	⇓	⇑	⇑	↓	**⇑**	**⇑**	**⇓**	⇑	⇑	⇑
	Branching coral	⇓	⇓ᵃ	⇓ᵃ	⇑	**⇓**	**⇓**	**⇑**	⇑	⇓	⇓

Arrow direction indicates trend (⇑ = positive, ⇓ = negative, ↔ = no relationship) and arrow thickness indicates significance (double line = $P < 0.05$, single line = $P < 0.10$). Group A indicates the observed trend for each variable in the FR sites versus the BR ones. Group B summarizes the HRA regression-level studies of each variable on growth (*G*), fecundity (*F*), and survival (*S*) separately. "n/a" indicates that HRA-level comparisons were not possible for this variable. Group C summarizes the expected relationship (positive ⇑, negative ⇓, or unknown ⇓⇑) between each variable and growth, fecundity and survival separately based on previous studies. Using the expected relationships from group C and the calculated (from this study) FR–BR trends for each demographic variable measured (growth, fecundity and mortality all higher on the FR) group D lists the expected FR relative to BR trend for each variable relative to growth, fecundity, and survival. These indicate where data do or do not support each mechanism

Bold arrows indicate instances where expected results for each demographic parameter match the observed trends

[a] Indicate variables included in the best-fit models from the multiple regression analyses (Table 4)

of each variable in the two reef zones based on the magnitude of the observed demographic differences in each reef zone (growth, fecundity and mortality all higher on the fore reef) and their expected relationship to each variable (as given in Table 5, group C). For instance, we would expect food availability to be positively associated with all three variables (growth, fecundity, and survival, Table 5, group C). The finding of this study that growth and fecundity are higher on the fore reef leads us to expect higher levels of food there if food is the controlling factor. Our finding that survival is lower on the fore reef leads to the opposite expectation. Using this logic we can compare the observed fore reef versus back reef trend (Table 5, group A) with these expected results (Table 5, group D) relative to each of the causative mechanisms and evaluate the degree to which the data support (bold arrows in Table 5, group D) or do not support each. Thirdly we add in the information resulting from the multiple regression best-fit models (Table 5, group B, arrows with superscript "a").

Using this as a summary, we see little indication that food supply is the driving factor behind these life history differences. We were unable to detect any differences in plankton supply to the two habitats in this study despite multiple trap deployments, variance minimizing arrangements, and long soak times. Preliminary studies on 24 fish from each habitat at 3 different times of day also failed to show any significant difference in the number of plank-tonic (or benthic) bites taken by fish between reef zones (see Lyman 2002 for data). Other studies (Levin et al. 2000) related food supply to growth and even mortality. Jones (1986) showed that elevated food supply increased growth of a common Great Barrier Reef Pomacentrid. Nemeth (1997) found higher growth and lower mortality of *S. partitus* in fore reef habitat compared to back reef in St. Croix and attributed these effects at least in part to food supply (which was significantly higher on the fore reef). Plankton supply in the Nemeth (1997) study may have been different due to depletion of plankton as the water mass carrying it washed over the reef. In the Florida

Keys, flow is predominately wind driven and along-shore (Lee and Williams 1999) and thus both sides of the reef are very likely exposed to similar water masses.

While intra-specific density-dependent survival has been demonstrated for other species of reef fish (see Hixon and Jones 2005 for a review) and even implicated in habitat differences in mortal-ity, longevity, and growth (Gust et al. 2002) we found no support for mechanisms associated with density-dependent effects in this study. While fore reef sites contain on the order of four times as many fish as back reef sites, the difference in the distribution of these fish (clumped on the back reef and random on fore reef) led to the same effective density and nearest neighbor distance in both habitats. Levin et al. (2000) observed similar distributional patterns for *S. planifrons*, in St. Croix, USVI. A concurrent study on our sites by Rilov et al. (2007) attributes the distributional patterns to the availability of visually "open" space (i.e., free of interference by branching and fan coral) which is in short supply on the back reef. Inter-specific competition does seem to be playing an important role in driving the observed differences in growth and fecundity, but not in survival. Levin et al. (2000) found similar results for the closely related *S. planifrons* in continuous versus patch reef habitat. They noted significantly higher growth rates in continuous habitat and hypothesized that it was due in part to lower aggression.

Predation is very often a powerful structuring force on coral reefs (Hixon and Jones 2005) and our results support this notion. But in this case it seems not to be the absolute density of predators which drives the process, but rather the relative predation pressure as mediated by the protection afforded by habitat. As indicated in Table 5, the rugosity, size, number of holes and percent massive and branch-ing coral all significantly related to growth, fecun-dity, or survival in some way. The best-fit model equations for both growth and fecundity indicated that each is negatively related to the percent of branching coral. This is possibly due to the reduced visual field associated with this type of habitat which causes more restricted movement due to a reduced ability to detect predators (Rilov et al. 2007). This reduced movement very likely

interferes with both feeding as well as courtship activities. *S. partitus* have been shown to reduce courting in the presence of a predator (Figueira and Lyman in press). This mechanism is likely also involved in the positive relationships with HRA size. Larger HRAs offer the possibility of increased visibility (important for courtship) and access to planktonic food resources while remaining close to protective habitat.

Mortality was most directly related (negatively) to the density of all holes, and specifically those with an aperture of less than 25 cm^2. This is the size Nemeth (1997) found to be most critical to growth and survival of *S. partitus*. It is probably the lack of suitable shelter combined with the less topographically complex structure of the fore reef habitat that increases the risk of predation there relative to the back reef zone. This same effect was seen for a wrasse in Okinawa by Karino et al. (2000) who found that predation risk was lower on a site with greater topographical complexity than on an adjacent site, despite the fact that frequency of encounters with predators was higher in the site with greater complexity.

Consequences of demographic variability

It appears that a combination of reduced competition and lower habitat complexity (on the shelter scale, i.e., small holes in rock or coral) on the fore reef results in fish there having higher growth and reproduction but reduced survival. With a mortality rate (z) of 0.0034, an adult back reef fish of either sex has a 10% chance of surviving two breeding years, while a fore reef fish with a mortality of 0.0083 has the same chance to survive only for one breeding year. Interestingly, an average male on the fore reef has just under twice the reproductive output (area of eggs per spawning day, Fig. 4) of a back reef male. This roughly equivalent life-time reproduction raises the possibility that *S. partitus* are exhibiting life history plasticity in response to differences in their local environment. Unfortunately the correlative nature of our study does not allow for this theory to be rigorously tested. But this would be a productive avenue for future research using transplant experiments.

The possibility that turnover is higher on the fore reef is intriguing as it represents the sum product of a host of demographic characteristics which could give such areas dramatically different dynamics from back reef areas, and which will strongly affect the relative contribution of populations in these habitats to the overall metapopulation (Figueira and Crowder 2006). For instance, average male per capita reproduction (clutch area/day spawning) was 1.5 times higher in fore reef sites and average abundance was 3.9 times higher there. Assuming no difference in sex ratio between habitats, this implies that per area output from a fore reef site would be about six times greater than from a back reef patch; and this does not account for the more rapid attainment of sexual maturity that likely occurs as a result of faster growth on the fore reef. The aggregate impact of such variation in a key demographic parameter, local production, on large-scale dynamics is likely to be important [though as Kritzer and Davies (2005) have pointed out for longevity, this is not necessarily straightforward]. Further study is warranted and these results emphasize the need to more closely evaluate local dynamics, even when very large-scale responses are of interest.

Robertson et al. (2005) has suggested that perhaps medium-scale variation is the rule for reef fish. Of course, the scale over which demographic rates may vary will be dependent upon the scale of movement of the organism (Williams et al. 2003). This study suggests that for more site-attached species, small-scale variability might also be common and that habitat-specific demographic rates might be more ubiquitous than we had previously imagined. Previous modeling efforts have shown the large influence that such local-scale demographic variability can have, both on the source–sink nature of an individual patch and on the overall metapopulation dynamics (Figueira and Crowder 2006). Thus habitat specific demographics deserve careful consideration and with continued study, can add greatly to our ability to understand these dynamic systems.

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