



Distribution, abundance, and microhabitat characterization of small juvenile corals at Palmyra Atoll

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ABSTRACT: Juvenile corals are an important component of the population dynamics of corals, but little is known about the ecology and natural history of their early life-history stages. In demographic surveys, small juvenile corals are often grouped with larger and older corals or overlooked entirely due to their small size and cryptic nature. This study describes the distribution, abundance, and microhabitat of small juvenile corals, defined as post-settlement corals ≤ 5 mm in diameter, at Palmyra Atoll, Central Pacific. A diver-operated pulsating blue light and filter system was used to enhance innate coral fluorescence during daylight to aid in detecting small juvenile corals. Juvenile densities ranged from 0 to 59.5 m⁻² and were more than 9 times higher on the fore reef (21.9 ± 0.8 m⁻²) than on the back reef (2.4 ± 0.3 m⁻²). The highest juvenile densities were observed in the middle of the sampled range at 14 m depth on the fore reef. Juvenile corals accounted for >31% of coral colonies in all habitats and depths, which resulted in positively skewed size-frequency distributions. The microhabitat of juvenile corals on coral rubble was best described as a convex surface covered with crustose coralline algae that lacked another coral within a 20 mm radius. This study provides basic ecology and natural history information of small juvenile corals and shows the feasibility of surveying corals ≤ 5 mm in diameter as a method for monitoring coral populations and assessing environmental changes on a coral reef.

KEY WORDS: Juvenile corals · Ecology · Distribution · Abundance · Microhabitat · Recruit · Palmyra Atoll

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INTRODUCTION

Coral reefs are in a state of global decline because of multiple stressors, including overfishing, poor water quality, and rising concentrations of carbon dioxide (Hughes 1994, Jackson 1997, Pandolfi et al. 2003, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007). Therefore, a better understanding of coral population biology is needed for coral reef assessment and management. Population dynamics and demographic analyses require accurate ecological information about all life-history stages, but little is known about the ecology of small juvenile corals (e.g. ≤ 5 mm in dia-

meter). Small juvenile corals, also termed recruits in some studies, are critical to the future of coral reefs because they become the foundation of a reef ecosystem, and are an important component of resiliency, a reef's ability to recover from disturbance (Bellwood et al. 2004).

Coral population data can be used to assess the health of coral reefs. For example, coral size-frequency distributions are used to infer the future trajectory of coral populations (Bak & Meesters 1998, 1999, Hughes & Tanner 2000, Smith et al. 2005). In demographic models, varying recruitment rates can change whether a coral population increases or decreases (Hughes &

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Tanner 2000, Edmunds & Elahi 2007). The ecology and population dynamics of early post-settlement corals are poorly understood because of challenges in surveying juvenile corals. Coral recruits are often ≤ 1 mm (Babcock et al. 2003), making them difficult to detect on a coral reef (Miller et al. 2000). A lack of data on the abundance of juvenile corals can lead to erroneous size-frequency distributions and inaccurate population models.

There are 3 principal reasons why previous juvenile coral studies provide inadequate information on the earliest life-history stage of corals: (1) Many studies defined juvenile corals broadly, grouping small and large juveniles together. In studies that randomly surveyed juvenile coral densities on natural substrates (e.g. Bak & Engel 1979, Rogers et al. 1984, Edmunds & Carpenter 2001), the most common definition for a juvenile coral was a coral ≤ 40 mm in diameter (Fig. 1). Occasionally, size detection limits are reported as low

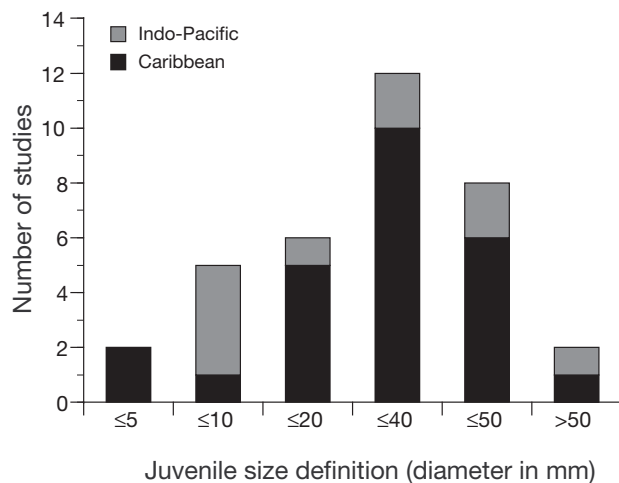


Fig. 1. The smallest juvenile size definition used in previous studies of juvenile coral density on natural substrates ($n = 35$). Studies were conducted in the Caribbean and Indo-Pacific. The definition was given as a diameter in the literature except for Smith (1992). For Smith (1992), the smallest size class (≤ 0.25 cm²) was converted to equivalent spherical diameter of ≤ 5.6 mm, which was placed in ≤ 5 mm category. (Sources: ≤ 5 mm: Smith 1992, Mumby 1999; ≤ 10 mm: Connell 1973, Harriott 1985, Babcock 1991, Hughes & Tanner 2000, Brown et al. 2002; ≤ 20 mm: Smith 1997, Kramer 2003, Ruiz-Zarate & Arias-Gonzalez 2004, Piniak et al. 2005, Smith et al. 2005, Vidal et al. 2005; ≤ 40 mm: Bak & Engel 1979, Colgan 1981, Rogers et al. 1984, Wittenberg & Hunte 1992, Chiappone & Sullivan 1996, Edmunds & Bruno 1996, Edmunds 2000, Edmunds & Carpenter 2001, Edmunds et al. 2004, Carpenter & Edmunds 2006, Glassom & Chadwick 2006, Edmunds & Elahi 2007; ≤ 50 mm: Rylaarsdam 1983, Bak 1987, Edmunds et al. 1998, van Woesik et al. 1999, Miller et al. 2000, Webster & Smith 2002, Moulding 2005, Sandin et al. 2008; > 50 mm: Dustan 1977, Tamelander 2002)

as 5 mm (Miller et al. 2000) or even 1 mm (Glassom & Chadwick 2006), but such small individuals are difficult to detect and are almost certainly underrepresented in these studies, as previously acknowledged (Miller et al. 2000, Glassom & Chadwick 2006). (2) Artificial substrates such as ceramic tiles are often used to study post-settlement recruits (Hughes et al. 1999, Mundy 2000, Fox 2004). Population dynamics on artificial substrates are substantially different than on natural reef substrates (Rylaarsdam 1983) because artificial substrates often lack appropriate chemical cues from biofilms and/or crustose coralline algae to which juvenile corals respond (Morse & Morse 1996). Furthermore, mortality on artificial substrates is much higher than on natural substrates (Rylaarsdam 1983). Hence, basic measurements of distribution and abundance on artificial substrates may differ from measurements on natural reef substrates because the population dynamics are likely to be dissimilar between the 2 environments. (3) Most previous studies of juvenile corals have been conducted on degraded coral reefs. Over 70% of the previous density studies, including the 2 previous studies that included a ≤ 5 mm size class (Smith 1992, Mumby 1999), were carried out in the Caribbean (Fig. 1), where significant reductions in the abundance of herbivores and carnivores began centuries ago, followed by major losses of architectural species beginning in the 1970s (Jackson 1997, Aronson et al. 2002, Gardner et al. 2003, Pandolfi et al. 2003). Thus, the importance of the present study was to provide ecological data on small juvenile corals on natural substrates of a healthy coral reef, thereby addressing the limitations of previous studies.

The objective of the present study was to characterize the distribution, abundance, and microhabitat of corals ≤ 5 mm in diameter using a novel modification of fluorescence techniques. Coral fluorescence has been used recently to help observe coral recruits, because both corals and their symbiotic dinoflagellates auto-fluoresce when excited with specific wavelengths of light. Past studies have shown that nighttime use of fluorescence techniques results in recruits being more easily observed than in traditional daytime searches (Piniak et al. 2005). Nighttime surveys using fluorescence techniques located 20 to 50% more coral recruits and smaller recruits compared to traditional daytime searches (Baird et al. 2006). However, night diving is logistically more complicated than day diving. The present study modified the fluorescence technique by adding a pulsating excitation light so that small corals would be easily detected during the day.

The present study was conducted at Palmyra Atoll ($5^{\circ} 52' N$, $162^{\circ} 06' W$), a US territory in the Northern Line Islands, Central Pacific (Fig. 2). Palmyra is characterized as a healthy coral reef community with a com-

plete food web, a predominance of crustose coralline algae and hard coral cover, and low biomass of fleshy algae (Sandin et al. 2008). There are 36 genera and 176 species of scleractinians found on Palmyra (Maragos et al. 2008b). Because of Palmyra's geographic isolation, restricted human presence, and recent protection by the US Fish and Wildlife Service, many localized sources of anthropogenic stress, such as overfishing, are absent. Despite some physical alterations to the atoll during World War II (Dawson 1959, Maragos et al. 2008a), Palmyra ranks as exceptionally healthy compared to most reefs (Knowlton & Jackson 2008).

MATERIALS AND METHODS

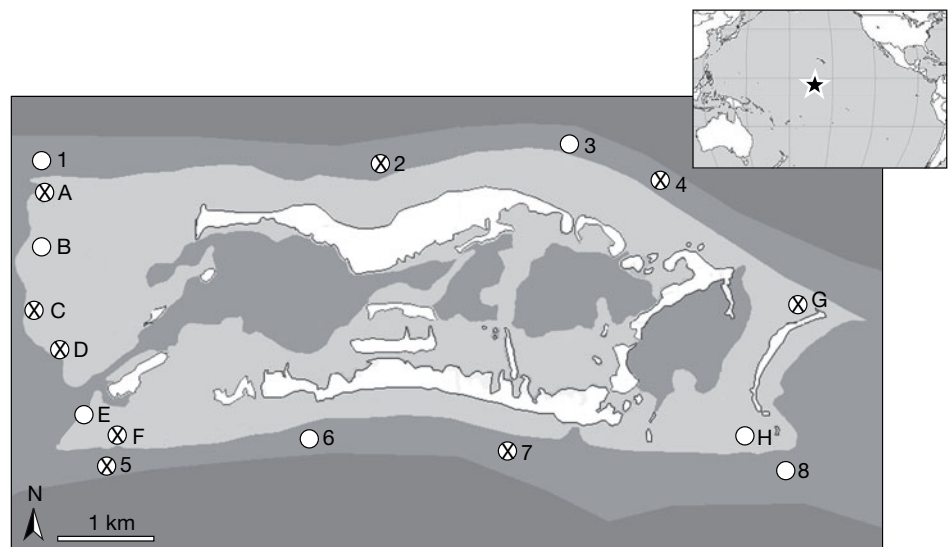
Study locations. Palmyra Atoll is exposed to considerable wave action and strong currents. Depending on the positioning of the Intertropical Convergence Zone, Palmyra lies within the North Equatorial Current or the North Equatorial Countercurrent (Hamann et al. 2004, Maragos et al. 2008b). The present study included atoll-wide surveys in both the fore reef and the back reef in August and September 2006 (Fig. 2). The fore reef was dominated by *Montipora* spp., *Pocillopora* spp., *Fungia* spp., *Pavona* spp., and *Porites* spp., while the back reef was dominated by *Montipora* spp., *Pocillopora* spp., *Pavona* spp., and *Acropora* spp. (M. S. Roth unpubl. data). Previous studies found 20 and 45% live coral cover on the fore reef (Sandin et al. 2008 and NOAA data reported therein). Eight fore reef sites were haphazardly chosen to span the north and south sides of the atoll, encompassing all sloping fore reef habitat. Each fore reef site was surveyed at 3 depths: 10, 14, and 18 m. Because of wave exposure, it was not

feasible to survey shallower depths on the fore reef, and that area was devoid of corals. The back reef primarily consisted of habitat on the western side of the atoll with 2 shallow pools on the eastern side of the atoll. Sites were haphazardly chosen to span the western side of the atoll, and at sites of interest including the Longline Wreck (Site D, Fig. 2) and the Northeast and Southeast Coral Gardens (Sites G and H, Fig. 2). On the shallow back reef, it was only possible to survey at 1 depth at each site, which varied from 1.5 to 4.9 m.

Detection of juvenile corals using pulsating fluorescence-aided visualization. In the present study, a small juvenile coral was defined as a post-settlement coral with its longest diameter ≤ 5 mm. Hereafter, small juvenile corals are referred to as juvenile corals. Any corals ≤ 40 mm are most likely to arise from sexual reproduction rather than asexual reproduction (Bak & Engel 1979) and were easy to distinguish from corals produced through asexual reproduction by growth and morphological characteristics.

When excited with blue light, both corals and their symbiotic dinoflagellates autofluoresce. Coral autofluorescence, which is primarily green but can also be other colors, is due to the presence of fluorescent proteins, while dinoflagellate red autofluorescence is due to chlorophyll. Autofluorescence was detected with a prototype lighting system (NightSea). The light (UK C4) was modified so that both bulbs were fitted with a custom blue interference filter to induce autofluorescence. In an improvement over previous fluorescence methods, one of the bulbs was customized to flash. A diving mask yellow barrier filter, which blocked the excitation light to the viewer, enabled the easy detection of corals including those on all sides of surfaces

Fig. 2. Study sites at Palmyra Atoll ($5^{\circ}52'N$, $162^{\circ}06'W$). Transect and quadrat surveys were conducted at all sites (O), and rubble surveys were conducted on a subset of sites (X). Fore reef sites are labeled from west to east: (1: Tortugonas, 2: North Beach, 3: Aviation, and 4: Quail on the north side of the atoll, and 5: Penguin Spit, 6: Paradise, 7: North South Causeway, and 8: Southeast Corner on the south side of the atoll). Back reef sites were labeled from north to south: (A: Tortugonas, B: Far North of Longline Wreck, C: North of Longline Wreck, D: Longline Wreck, E: Penguin Spit Permanent, F: Penguin Spit Mid on the west side of the atoll, G: Northeast Coral Gardens, and H: Southeast Coral Gardens on the east side of the atoll)



and in crevices. The pulsating excitation light caused corals <1 mm in diameter to 'blink' conspicuously, even in daylight. Because other reef organisms fluoresce, it was necessary to discriminate small corals from similar-looking organisms such as anemones and zoanthids, which were soft when probed compared to corals. The only coral species observed without autofluorescence was the azooxanthellate *Tubastrea* sp.; additionally hydrocorals in the genus *Stylaster* lacked autofluorescence. There have been observations of non-fluorescent morphs of coral species (Salih et al. 2000, Baird et al. 2006).

Transect and quadrat surveys. The fore reef and back reef of Palmyra Atoll were surveyed using transects and quadrats. Quadrats with a circular area of 0.24 m² were placed every 5 m along 50 m transects of constant depth. All scleractinian corals inside or partially inside a quadrat were counted and binned into size classes using longest diameter as the size criterion. As described in the previous paragraph, a pulsating blue light with a barrier filter was used during the daytime to facilitate detection of the smallest corals. Because the lighting system was intended to enhance detection of juvenile corals, corals were counted whether they were detected under blue light or sunlight. Because it was not possible to taxonomically identify small juvenile corals, surveys represent the whole coral community. At each fore reef site 9 to 11 quadrats were sampled, and 11 quadrats at each back reef site.

Rubble surveys. To determine the microhabitat characteristics of juvenile corals, coral rubble pieces were collected and carefully examined for juvenile corals using white and blue light and a stereomicroscope. Two 5 gallon (19 l) buckets of rubble from the top ~10 cm of the reef were collected at each site, and the volume of rubble collected determined by water displacement. A subset of back reef and fore reef sites (Fig. 2) were surveyed for logistical reasons. All sides of the rubble were examined but it was not feasible to record the orientation of each piece of rubble. The size of each coral was measured with vernier calipers and the coral microhabitat was described by the surface geometry, substrate material and proximity to other corals. The geometry was defined by the surface plane on which the coral was lying: convex surface, depression (concave surface), hole/crevice (cavity in the surface), or cryptic (other non-exposed surfaces such as between branches). The substrate material was recorded as anything underneath the coral; when a coral was lying on crustose coralline algae and bare space, both were included. A coral was categorized as having a coral neighbor if there was a coral within 20 mm of its perimeter. The microhabitat characteristics of 2 size classes of corals (≤ 1 and 4–5 mm) were

compared using the frequency distributions of microhabitat data.

Statistical analyses. Statistical analyses were conducted using JMP version 7.0 and R software version 2.2.1. A 2-way ANOVA (site and depth) was used to test for differences in juvenile densities on the fore reef. A 1-way ANOVA (site) was used to test for differences in juvenile densities in the back reef. To compare the fore reef and back reef communities, data from fore reef (all depths) and back reef were used in statistical analyses. Unpaired *t*-tests were used to compare fore reef and back reef juvenile densities. Juvenile densities were expressed as mean \pm SE. Size-frequency histograms were created from ln-transformed data, and compared to normal distributions based on the characteristics of the data using the Kolmogorov-Smirnov test (Bak & Meesters 1998, 1999). Skewness was calculated from transformed data and its significance was determined by a comparison with the skewness of 10 000 replicates of resampling a normal distribution with the same sample size. Pearson's χ^2 tests were used to test for differences in microhabitat (geometry and substrate) frequency among juveniles from different depths on the fore reef. Pearson's χ^2 test with Yates continuity correction was used to compare juvenile neighbor microhabitat data from different depths on the fore reef. Additionally, Pearson's χ^2 test was used to test for differences in microhabitat between ≤ 1 and 4–5 mm corals. Back reef juvenile corals in the rubble surveys were not included in statistical analyses because of low sample size. Statistical significance was based on an $\alpha = 0.05$ level.

RESULTS

Coral size-frequency distribution

Juvenile corals constituted a substantial proportion of the total coral population (Table 1). The proportion of juveniles was much larger on the fore reef ($34.7 \pm 0.9\%$) than the back reef ($8.6 \pm 0.1\%$). The coral population at Palmyra Atoll was dominated by smaller corals (Fig. 3). Logarithmic transformations of neither the fore reef nor the back reef coral population size frequencies were normally distributed ($p < 0.001$ for each); both were significantly right- (positive) skewed, with skewness values of +1.22 ($p < 0.001$) and +0.72 ($p < 0.001$), respectively. On the fore reef, the size distribution was significantly right-skewed at each depth examined: +1.13 ($p < 0.001$) at 10 m, +1.29 ($p < 0.001$) at 14 m, and +1.21 ($p < 0.001$) at 18 m. These results indicate that each habitat contained more small corals than would be predicted by a normal distribution (Fig. 3).

Table 1. Juvenile coral (≤ 5 mm) density and percentage of total corals. N: number of quadrats. Data are mean \pm SE

Habitat	N	Density (m^{-2})	% of total corals
10 m fore reef	86	17.05 \pm 1.06	33.7 \pm 0.7
14 m fore reef	82	30.13 \pm 1.64	36.7 \pm 0.6
18 m fore reef	78	18.60 \pm 1.10	32.6 \pm 0.7
Total fore reef	246	21.90 \pm 0.77	34.7 \pm 0.9
Back reef	88	2.41 \pm 0.30	8.6 \pm 0.1
Total	334	16.77 \pm 0.61	31.1 \pm 0.3

Juvenile coral distribution and abundance

In the transect and quadrat surveys, a total of 1338 juvenile corals were counted in 80.16 m^2 reef sampled. Average juvenile density on the fore reef was over 9 times higher and statistically different than the back reef ($t_{332} = 7.4$, $p < 0.001$; Table 1). On the fore reef, both depth ($F_{2,222} = 7.4$, $p < 0.001$) and site ($F_{7,222} = 4.4$, $p < 0.001$) had a significant effect on the juvenile density, but the interaction between depth and site was not significant ($F_{14,222} = 1.2$, $p = 0.26$; Fig. 4A). Average density was highest at mid-depths (14 m), with shallower (10 m) and deeper (18 m) depths having densities of 43 and 38% respectively of densities observed at mid-depths. The highest recorded juvenile density was $59.5 \pm 8.3 m^{-2}$ at Site 5 (Penguin Spit) at a depth of 14 m. The southern sites (Sites 5 to 8, Fig. 2) had higher densities of juvenile corals that were significantly different from the northern sites (Sites 1 to 4; $t_{244} = 2.8$, $p < 0.01$), but there was no difference in densities between western (Sites 1, 2, 5, and 6) and eastern sites (Sites 3, 4, 7, and 8; $t_{244} = -0.6$, $p = 0.52$). On the back reef, there were 2 sites without juvenile corals. There were no sig-

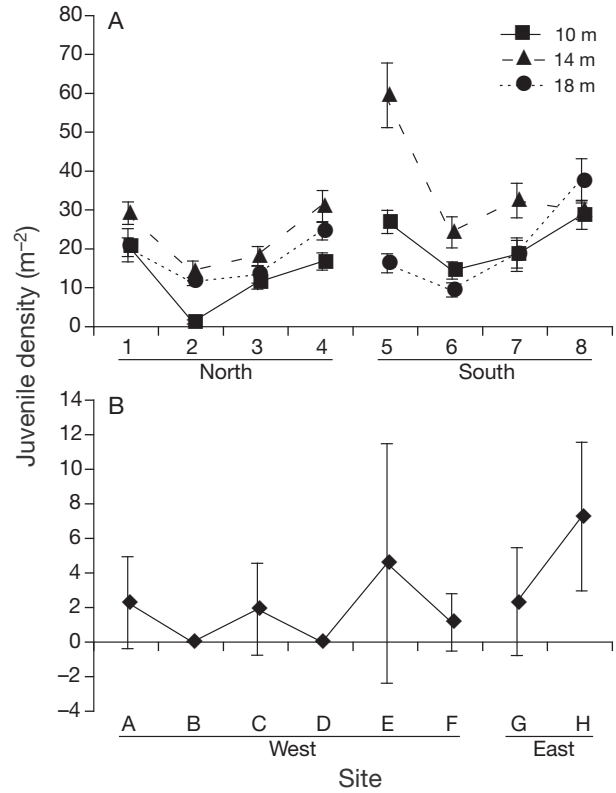


Fig. 4. Juvenile coral (≤ 5 mm in diameter) densities at the (A) fore reef by depth and site and (B) back reef by site. Data are mean \pm SE. See Fig. 2 legend for site codes

nificant differences in juvenile densities among back reef sites ($F_{7,80} = 2.1$, $p = 0.05$; Fig. 4B).

The coral rubble surveys showed similar juvenile distribution and abundance patterns to the transect and quadrat surveys. We sampled 114 l of coral rubble

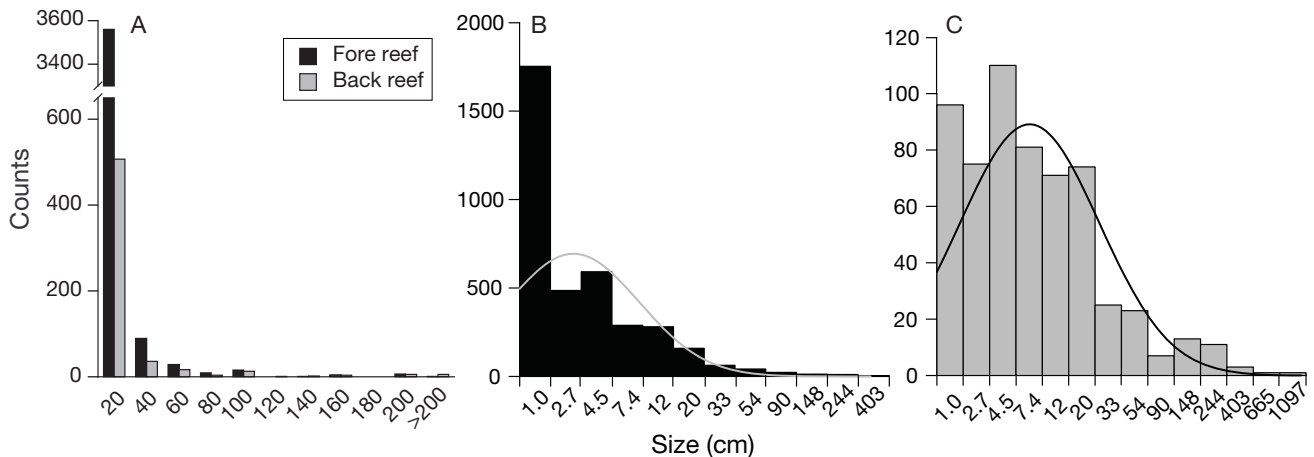


Fig. 3. Size distribution of corals. (A) Untransformed size-frequency distribution on the fore reef ($n = 3713$) and the back reef ($n = 591$). Size-frequency distribution of logarithmically transformed data on (B) the fore reef and (C) the back reef. In (B) and (C), the curve represents the normal distribution. Coral distributions were significantly right-skewed ($p < 0.001$) and significantly different from the normal distribution ($p < 0.001$ for each). Labels on the x-axis were represented by their endpoints (e.g. 20 represents 0–20 and 40 represents 20.01–40)

from 4 fore reef sites and 5 back reef sites. On the fore reef, most juvenile corals (45.7%) were found at the mid-depth of 14 m, followed by 18 m (40.9%) and 10 m (13.4%). As with the density data, more juveniles were observed in the fore reef rubble ($n = 314$) than the back reef rubble ($n = 8$).

Juvenile coral microhabitat

Based on microhabitat analysis of 314 juvenile corals obtained from the fore reef coral rubble, most juvenile corals were found on convex surfaces, rather than in depressions, holes/crevices, or other cryptic locations (Fig. 5A), a pattern that was not affected by depth ($\chi^2 = 6.7$, $p = 0.35$). Corals were predominately located on crustose coralline algae, followed by bare space at all depths (Fig. 5B). Surprisingly, >12% of corals were found on the brown encrusting alga *Lobophora* sp. The substrate characteristic patterns were not significantly different between samples collected from 14 and 18 m ($\chi^2 = 3.0$, $p = 0.38$). These patterns were generally similar to substrate characteristics from corals collected from 10 m, but the crustose coralline algae microhabitat was less dominant ($\chi^2 = 24.2$, $p < 0.001$). Just under

half (48%) of the corals had a coral neighbor within a 20 mm radius.

The microhabitats of corals ≤ 1 and 4–5 mm were not statistically different. The ratio of substrate geometries (convex:depression:hole/crevice:other cryptic) for ≤ 1 mm corals was 41:21:10:11 and for 4–5 mm corals was 42:11:8:5 ($\chi^2 = 3.7$, $p = 0.29$). The distribution of substrates (crustose coralline algae:bare:*Lobophora* sp.:other) for ≤ 1 mm corals was 58:32:10:2 and for 4–5 mm corals was 48:34:10:6 ($\chi^2 = 2.9$, $p = 0.40$). The distribution of neighbors (with:without) for ≤ 1 mm corals was 37:46 and for 4–5 mm corals was 29:36 ($\chi^2 = 0.03$, $p = 0.87$).

Too few juveniles were found on the back reef for statistical analyses of their microhabitat characteristics. Qualitatively, back reef juvenile corals appeared to have similar microhabitat distributions as fore reef corals.

DISCUSSION

The present study used a modified fluorescence technique to make extensive daytime observations of juvenile corals. The equipment required was low-tech, easy to use while SCUBA diving, and affordable for scientists and managers. Coral species that have non-fluorescent morphs may be more difficult to detect and could be underrepresented in these surveys. However, this methodology significantly enhanced the ability to detect small corals that are otherwise difficult to observe and enabled a thorough investigation of the distribution, abundance, and microhabitat of small corals.

The microhabitat data confirmed what is well known—that juvenile corals prefer crustose coralline algae and bare space (Morse & Morse 1996, Harrington et al. 2004)—but provided some surprising results. Most intriguing was that *Lobophora* sp. was chosen as a substrate for coral settlement and that large (4–5 mm) and small juveniles (≤ 1 mm) had similar distributions in this regard. This suggests that *Lobophora* sp. did not affect juvenile survivorship at these size classes, perhaps questioning the negative effects of macroalgae on juvenile corals on some reefs. Evidence of these negative effects includes macroalgae decreasing juvenile coral settlement, growth rates, and survivorship in some species (Lirman 2001, Birrell et al. 2005, Box & Mumby 2007). However, neither settlement rates nor survivorship of coral larvae from *Favia fragrum* were negatively affected by settling on the green alga *Halimeda opuntia*, nor was development of the recruits affected over 5 d (Nugues & Szmant 2006). It is likely that the competition between coral and algae could be affected by nutrients and herbivory (Jompa & McCook 2002).

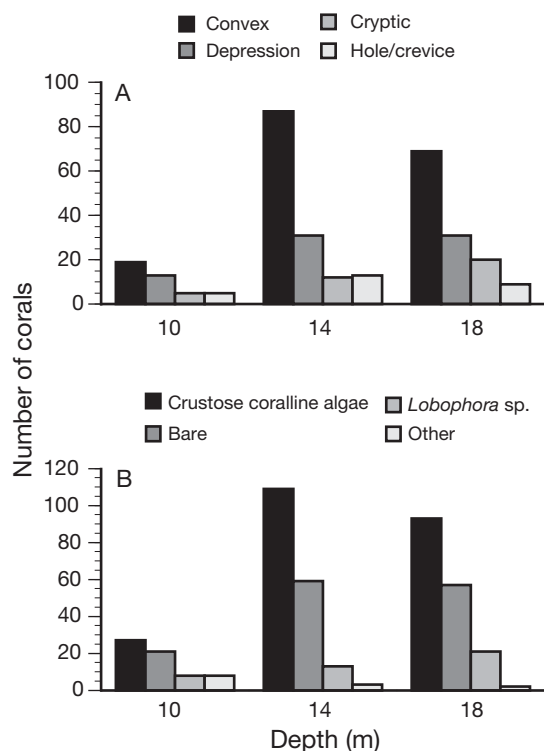


Fig. 5. Microhabitat characteristics, (A) geometry and (B) substrate, of juvenile corals (≤ 5 mm in diameter) on coral rubble from the fore reef. See 'Materials and methods' for description of surface geometry

In contradiction to what was anticipated, the distribution of microhabitat substrates was identical between ≤ 1 and 4–5 mm corals. These results may challenge previous assumptions of the effects of microhabitat on recruit survivorship (Caley et al. 1996), including geometry (Sammarco 1980), substrate (Harrington et al. 2004), and competition (Sammarco 1991). Other studies have also reported a lack of strong correlation between microhabitat (orientation of substrate) and survivorship in the Caribbean (Edmunds et al. 2004) and on the Great Barrier Reef (Babcock & Mundy 1996), despite selection for particular microhabitats.

Juvenile coral (≤ 5 mm) densities on the fore reef at Palmyra Atoll were highest at mid-depths of 14 m, possibly representing a balance between considerable wave exposure at shallower depths and less solar irradiance at deeper depths. Palmyra receives different currents depending on the time of year (Hamann et al. 2004, Maragos et al. 2008b), which may have contributed to a more homogeneous environment. Studies on small-scale flow around Palmyra during coral spawning times could elucidate the spatial patterns of coral recruitment, particularly because coral recruitment can vary considerably in space and time (Hughes et al. 1999). The much lower densities on the back reef compared to the fore reef may have resulted from differences in biological communities or environmental conditions including human alterations to the hydrodynamics due to prior construction during World War II (Dawson 1959, Maragos et al. 2008a).

The 2 other studies of juvenile corals ≤ 5 mm, which were conducted in the Caribbean (Fig. 1), reported lower densities than those observed on the reefs of Palmyra Atoll (Smith 1992, Mumby 1999). Smith (1992) recorded juvenile densities up to ~ 24 m^{-2} in Bermuda (data estimated from size-class distribution in Smith 1992, their Fig. 2); Mumby (1999) reported juvenile densities up to ~ 0.6 m^{-2} in Belize, compared to 59.5 m^{-2} in the present study. The disparity in juvenile densities between the present study and these 2 previous studies could have many causes, including the state of reef degradation surveyed, the equipment used to detect juvenile corals, and the ocean basin.

To compare juvenile density estimates with previous studies that have defined juvenile corals as ≤ 40 mm in diameter, results were re-calculated using the same size class. At Palmyra, densities of corals ≤ 40 mm on the back reef (13.4 ± 1.1 m^{-2}) and fore reef (50.7 ± 1.3 m^{-2}) were significantly different ($t_{332} = 7.7$, $p < 0.0001$; Fig. 6). Corals ≤ 5 mm in diameter represent nearly 20% and over 40% of the juveniles (≤ 40 mm) on the back reef and fore reef, respectively. The densities of juveniles (≤ 40 mm) on the fore reef of Palmyra (41.5 to 67.0 m^{-2}) were among the highest recorded in the literature (Table 2). Another study that reported high

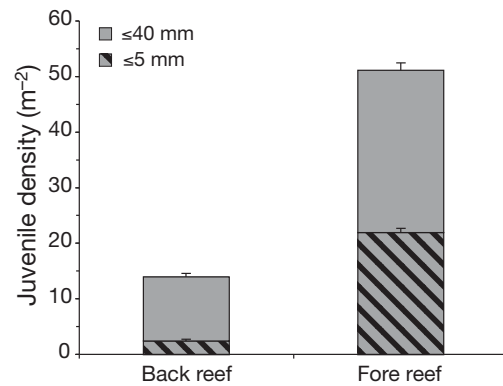


Fig. 6. Densities of juvenile corals using size criteria ≤ 40 mm and ≤ 5 mm. Data are mean \pm SE

densities of juvenile corals (42 to 173 m^{-2}) at sites selected with medium-to-low adult coral cover was in the Red Sea (Glassom & Chadwick 2006). Interestingly, the proportion of juvenile corals to the total coral population was ~ 10 to 27%, similar to that of the present study.

Juvenile corals accounted for a substantial proportion of the coral population; corals on the fore reef ≤ 5 mm in diameter represented over one-third of all corals. Correspondingly, size-frequency distributions from these data provide a perspective on what a healthy coral reef atoll may look like when all corals including the smallest size classes are surveyed. The size frequencies have a significant positive skewness, indicating a high proportion of small corals, which was also found during a recent study at Palmyra Atoll (Sandin et al. 2008). Surveys of healthy and degraded reefs in the Line Archipelago showed the same patterns in size-frequency distributions of corals (Sandin et al. 2008). However, the most degraded reef had fewer corals in the smallest size class and zero corals in the largest size class, but these distinctions were not captured in the size-frequency distribution analyses.

However, positive skewness of size distributions can be difficult to interpret. It may reflect a high proportion of juvenile corals, which is likely to be an important component of coral reef health, but it could also represent a declining population. Mortality and partial mortality of corals caused by disease, bleaching, or predation reduces colony size and causes fission of large corals. Positive skewing of coral populations in degraded habitats has been reported in the Caribbean (Hughes & Tanner 2000, Edmunds & Elahi 2007) and in the Indian Ocean (McClanahan et al. 2008), and predicted from *Acanthaster planci* predation disturbance models of the eastern Pacific (Fong & Glynn 1998). In contrast, Bak & Meesters (1998, 1999) proposed that a negatively skewed size-frequency distribution mod-

Table 2. Comparative table of mean juvenile coral densities using the standard definition of juvenile corals of ≤ 40 mm in diameter (in descending order of density). C. = central, USVI = US Virgin Islands, W. = western

Juvenile density (m^{-2})	Depth (m)	Reef habitat	Location	Ocean/sea	Source
67.0	14	Fore reef	Palmyra Atoll	C. Pacific	Present study
43.6	18	Fore reef	Palmyra Atoll	C. Pacific	Present study
42–173	5	Patch reef	Eilat, Israel	Red Sea	Glassom & Chadwick (2006)
41.5	10	Fore reef	Palmyra Atoll	C. Pacific	Present study
~24	4.5–8.5	'Urchin' zone	Jamaica	Caribbean	Edmunds & Carpenter (2001)
~17	3–37	Drop-off zone	Netherlands Antilles	Caribbean	Bak & Engel (1979)
13.3	1.5–4.9	Back reef	Palmyra Atoll	C. Pacific	Present study
13, 33	9	Submarine canyon	St. Croix, USVI	Caribbean	Rogers et al. (1984)
10.5–18.1	6	Fringe reef	St. John, USVI	Caribbean	Edmunds & Bruno (1996, pers. comm.)
~8 ^a	14–26	Exposed fore reef	Florida	Caribbean	Edmunds et al. (2004, pers. comm.)
6.3–43.7	1–6	Fringing reef	Barbados	Caribbean	Wittenberg & Hunte (1992)
5.35–12.3	6–16	Submarine terrace	Guam	W. Pacific	Colgan (1981)
5.2–17.9	10	Fore reef	Jamaica	Caribbean	Edmunds & Bruno (1996)
4.5–12.7	16–33	Seaward slope	Guam	W. Pacific	Colgan (1981)
~4–32 ^a	5	Fringing reef	St. John, USVI	Caribbean	Edmunds (2000)
3.2–7.75	1–6	Reef front	Guam	W. Pacific	Colgan (1981)
3–42	18, 27, 37	Submarine canyon	St. Croix, USVI	Caribbean	Rogers et al. (1984)
2.5–32.3	<6	Outer fore reef	St. Croix, Barbados, Bonaire, Belize, Jamaica, Grenada	Caribbean	Carpenter & Edmunds (2006)
1.18–3.74	2.7–18.6	Spur/groove, reef flat	Florida	Caribbean	Chiappone & Sullivan (1996)
0–0.15	5, 9	Fringing reef	St. John, USVI	Caribbean	Edmunds & Elahi (2007)

^aMean density was estimated from graphs given in $0.25 m^{-2}$

eled by a log-normal distribution inferred an unhealthy coral population. They hypothesized that disturbances increased mortality of smaller colonies and coupled with recruitment failure resulted in the predominance of larger colonies. Positively skewed size-frequency distributions were observed in the present study because we surveyed a healthy coral reef using a novel method to aid in detecting small juveniles. These data suggest that healthy reefs may be positively skewed, and with degradation become normally distributed and with further degradation become negatively skewed.

Because changes in coral size-frequency distributions can result from multiple factors, purely examining relative size frequencies to infer status of a coral population can be misleading. We suggest that, in addition to relative size-frequency data, it is important to compare the absolute numbers in each size class with particular attention to the smallest and the largest size class of corals. In addition, distinguishing recent settlers from the small remains of once-large colonies can help determine the processes underlying the size patterns observed.

Juvenile coral investigations not only provide relevant ecological data for coral population dynamics, but also could be useful as an indicator of environmental changes. Size-frequency distributions could be particularly relevant for coral reefs that do not have a well-established baseline of coral populations, yet still pro-

vide insight into a reef's resiliency and its future. A standardized procedure for surveying juvenile corals is needed so that data between locations will be comparable (Abelson & Gaines 2005). Daytime coral fluorescence surveys are effective, technologically simple, and affordable, providing a new capability for investigations of coral reef biology. Using fluorescence to aid finding juvenile corals should be part of the standardized technique to ensure reliable data on the smallest life-history stage.

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