REPORT

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Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA

Abstract Coral communities of Biscayne National Park (BNP) on offshore linear bank-barrier reefs are depauperate of reef corals and have little topographic relief, while those on lagoonal patch reefs have greater coral cover and species richness despite presumably more stressful environmental regimes closer to shore. We hypothesized that differences in rates of coral recruitment and/or of coral survivorship were responsible for these differences in community structure. These processes were investigated by measuring: (1) juvenile and adult coral densities, and (2) size-frequency distributions of smaller coral size classes, at three pairs of bank- and patch-reefs distributed along the north-south range of coral reefs within the Park. In addition, small quadrats (0.25 m^2) were censused for colonies < 2 cm in size on three reefs (one offshore and one patch reef in the central park, and one intermediate reef at the southern end), and re-surveyed after 1 year. Density and size frequency data confirmed that large coral colonies were virtually absent from the offshore reefs, but showed that juvenile corals were common and had similar densities to those of adjacent bank and patch reefs. Large coral colonies were more common on inshore patch reefs, suggesting lower survivorship (higher mortality) of small and intermediate sized colonies on the offshore reefs. The more limited small-quadrat data showed similar survivorship rates and initial and final juvenile densities at all three sites, but a higher influx of new recruits to the patch reef site during the single annual study period. We consider the size-frequency data to be a better indicator of juvenile coral dynamics, since it is a more time-integrated measurement and was replicated at more sites. We conclude that lack of recruitment does not appear to explain the impoverished coral communities on offshore bank reefs in BNP. Instead, higher juvenile coral mortality appears to be a dominant factor structuring these communities.

Key words Coral recruitment · Florida · Juvenile corals

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Introduction

Biscayne National Park (BNP) lies at the northern fringe of the Florida reef tract, and indeed at the northern latitudinal fringe of Atlantic coral reef distribution. Many seemingly suitable offshore bank-barrier reef habitats within the Park have very low relief and coral cover, while many lagoonal patch reefs have greater cover and richness of corals (Table 1). Paradoxically, the physical environment of the lagoonal areas, with greater terrestrial and bay influence, appears to be more, not less stressful for corals in terms of temperature and turbidity (Table 1). One possible explanation for the lower adult coral abundance on the bank-barrier reefs is a lack of coral recruitment at these sites (Porter and Meier 1992).

Studies of coral recruitment in the Caribbean have found variable rates of recruitment of predominantly small species which brood their larvae, especially *Agaricia agaricites* and *Porites astreoides* (Bak and Engle 1979; Rogers et al. 1984; Smith 1992, 1997; Chiappone and Sullivan 1996). These studies observed low recruitment rates by large frame-building species, most of which are broadcast spawners (e.g., *Montastraea* spp.,

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Table 1 Environmental and biotic characteristics for sites examined in this study (Weil et al., unpublished data). Patch reefs are in lagoonal areas while bank reefs make up the outer reef line. *Extreme temp.* indicates percent of days monitored when average temperature was above 30 °C or below 20 °C. *Sediment deposition* indicates mean of 13 2-week trap deployments

Sites	East Bache*	Triumph	Alina's*	Pacific	Elkhorn	Ball Buoy	Isa's*
Latitude (N)	25°28.98	25°28.31	25°23.20	25°22.18	25°21.78	25°18.52	25°19.91
Longitude (W)	80°08.44	80°06.72	80°09.77	80°08.36	80°09.94	80°11.99	80°11.87
Depth sampled (m)[a]	1–5	3–7	2–6	2–10	1–5	2–8	2–6
Reef type	Patch	Offshore bank	Patch	Offshore bank	Patch	Exposed patch/bank	Patch
Coral cover (%)	19.4	2.0	15.1	1.9	9.5	12.7	12.1
Coral species richness	40	23	39	28	29	40	43
Coral density (colonies/m^2)	7.7	2.8	10.0	4.4	10.6	10.3	11.8
Extreme temp.	3.1	1.2	2.8	n.a.	n.a.	0.4	3.4
Sediment deposition (mg/cm^2/day)	3.1	3.4	3.5	4.5	8.8	14.2	1.8
Estimated underwater visibility (m)[b]	n.a.	12	6	n.a.	n.a.	11	n.a.

* These reef names are colloquial and are not found on official charts
[a] The depth range of the two offshore bank reefs extends to ca. 25 m, but all the work conducted in this study was limited to the shallow depths comparable to those of the patch reefs
[b] Bohnsack et al. 1992

Acropora spp., *Diploria* spp., *Siderastrea siderea*; Szmant 1986). Porter and Meier (1992) reported no sexual recruitment of massive scleractinian corals in photoquadrats at Triumph and Ball Buoy reefs in BNP from 1989 to 1991 while artificial settlement plates at these sites yielded only 0.6 to 1.9 settlers m^{-2} year^{-1} (J. Tougas pers. Comm). In the Pacific, where recruitment patterns are often dominated by spawning *Acropora* spp., it has also been suggested that recruitment at high latitude sites is relatively low and dominated by brooding species (Harriot and Banks 1995; Hughes et al. 1999). Thus, it is plausible that impoverishment of coral communities at the high latitude bank reefs in BNP may be attributable to low recruitment.

The current study investigated pattern of recruitment (densities of pre-reproductive size classes) in order to discern its role in maintaining observed differences in coral community structure of BNP reefs. Juvenile densities ("standing stock of recruits"), colony size frequencies for four scleractinian species, and recruitment rates for scleractinian corals were compared between the depauperate offshore bank reefs and lagoonal patch reefs with higher coral cover, to determine if a lack of scleractinian recruitment precludes significant coral development on the bank-barrier reefs.

Materials and methods

Site descriptions

The outer reef line of the northern Florida Reef tract is comprised of a series of linear reefs that formed on morphological features of Pleistocene origin, with minimal Holocene deposition (Shinn 1988; Shinn et al. 1977, 1989 and pers. comm.). In the lagoon behind these outer reefs, there are over 3000 patch reefs of Holocene origin (Jaap 1984). Towards the southern end of the Park, there is a large break in the line of barrier reefs, from Pacific Reef south to Carysfort Reef (at the boundary of the Florida Keys National Marine Sanctuary). In this area, the Holocene patch reefs are more exposed to oceanic
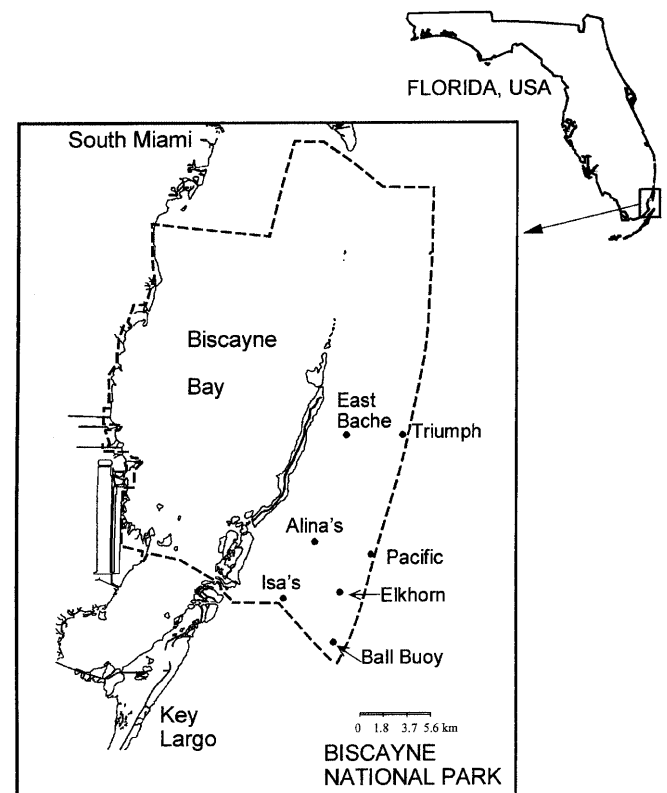

Fig. 1 Map of Biscayne National Park showing names and approximate location of study sites. See Table 1 for exact coordinates and other characteristics of each site

energy, and thus have more spur and groove development than the patch reefs in the central area of the Park. Seven reefs within BNP were examined in the current study (Fig. 1, Table 1). These sites included two patch reef/bank reef pairs in the central (East Bache and Triumph, respectively) and south-central (Alina's and Pacific, respectively) regions of the Park and a group of three reefs in the southern region (one lagoonal patch reef, Isa's, and two larger, more exposed patch reefs with some spur and groove formation, Elkhorn

and Ball Buoy Reefs). Elkhorn is somewhat protected from wave energy by Pacific Reef, while Ball Buoy has no offshore protective barrier. Thus, Ball Buoy is larger and more elongated than a typical BNP patch reef, and more like a bank reef, but it lacks the well-developed spur and groove formation typical of true bank reefs (Jaap 1984). We therefore refer to Ball Buoy in this study as an intermediate reef, by which we mean a reef of an intermediate structure between a patch reef and a bank reef.

Sampling of juvenile coral densities

Standing stock of juvenile corals was determined at each site. Twenty 1 m^2 quadrats per transect were sampled at 2- to 4-m intervals along each of four (on the smaller patch reefs: East Bache, Alina's and Isa's) or five transect lines per reef placed 20- to 25-m apart (total of 75 to 100 m^2 sampled per site). Abundance and cover of juvenile and adult coral colonies were recorded for each quadrat. For the purposes of this sampling procedure, juveniles were defined to be less than 5 cm in diameter for large species such as the *Montastraea* spp., *Diploria* spp., and *Siderastrea siderea*, or less than 2 cm in diameter for small-sized species (e.g. *Porites astreoides*, *Favia fragum*) according to the different minimum reproductive sizes for these large and small species (Bak and Engle 1979; Szmant 1986, unpubl. data; Wittenberg and Hunte 1992). This distinction complicates the data, and could conceivably bias the representation of certain species since 2-cm juveniles may be more often over-looked than 5-cm juveniles. However, this bias should be consistent between sites, and was necessary since a 5-cm colony of *Favia fragum* is a fully reproductive adult while a similarly sized colony of *M. faveolata* is not (Szmant-Froelich 1985). The lower size limit of detection for this method is estimated to be approximately 0.5 cm in diameter.

For older adult corals, it is recognized that colony size is not always a good indicator of age because of partial mortality and fragmentation, and thus a small coral may not necessarily be a young recruit (e.g. Hughes and Jackson 1980). However, in the present case, care was taken to distinguish between small colonies that were juveniles resulting from sexual recruitment and small ramets resulting from partial mortality or reattachment of adult fragments. The data for the latter two colony types are not reported here.

This data set displayed highly significant non-normality (Shapiro Wilkes test $P < 0.0001$) that was not alleviated by transformation. Thus, Kruskal-Wallis non-parametric ANOVAs followed by Dunn's post-hoc pairwise tests were conducted to test for significant differences among the seven sites in juvenile coral density and in the proportion of juveniles in the total coral population.

Colony size frequency distributions

Size frequency distributions of four common species of mounding hermatypic corals were measured at the two offshore bank reefs (Pacific and Triumph), two of the patch reefs, (East Bache and Isa's) reefs and at Ball Buoy, the intermediate reef. The species sampled included the three most common framework-building species in this area (*Siderastrea siderea*, *Montastraea cavernosa*, and *M. faveolata*), and *Porites astreoides*, an abundant but smaller mounding coral. All colonies of each species observed within 3 m on either side of the transect lines (see previous section for details) were measured, striving to obtain a sample size >100 for each species. Care was taken not to overlook small colonies. At some sites, one or more species were so rare that sample sizes were less than the desired 100 (noted on graphs) even though large areas of reef were examined (>750 m^2 for each site). No data are presented for *M. faveolata* at Triumph and Pacific reefs since only three and zero colonies, respectively, were encountered at these sites.

Sizes presented are based on a measurement made with a flexible measuring tape laid flush along the longest diameter of the colony. This measurement does not relate directly to surface area but rather provides an integration of both vertical and lateral growth (i.e. volume or total skeletal accretion of the colony).

Chi-squared contingency table analyses were used to test, for each species, the hypothesis that the size-frequency distributions differed significantly among sites. For some species, this test required combining the two or three largest or smallest size classes in order to avoid an excessive number of cells with expected frequencies less than five.

Permanent quadrats

We closely examined permanently marked quadrats (0.25 m^2 delimited with nails driven into the reef substrate), at several sites with extensive in-situ search procedures, including fanning away sediment and using magnifying glasses. Initial census and mapping of these plots allowed an assessment of the density of juvenile corals in each plot. A re-census (after 1 year) allowed determination of the subsequent recruitment rate, as well as the survivorship of the initial juveniles during that 1-year time interval. However, in order to accurately find and relocate recruits (0.1–2 cm in these quadrats), we were obliged to select areas with relatively flat substrate and without macro-organisms such as adult corals, gorgonians, sponges, or frondose macro-algae. Algal turf and small invertebrates were clearly present within our quadrats. This may have introduced some bias into the recruitment we observed as cryptic habitat was reduced in our sample (compared with the overall reef).

Because of the lengthy amount of underwater time these intensive searches required, we were limited to doing them at only three sites, East Bache (patch reef), Triumph (offshore bank-barrier reef), and Ball Buoy (intermediate). Ten quadrats were established at Triumph and Ball Buoy, and 15 quadrats at East Bache. The quadrats were first censused during the fall of 1994 (after the summer mass spawn) and re-censused 1 year later in November 1995.

Four parameters were analyzed for differences between sites: initial standing stock of juveniles (first census), rates of mortality of initial recruits, the rate of new recruitment over the 1 year interval, and the final standing stock (density at the second census). Each of the four parameters was analyzed in a separate Kruskal-Wallis non-parametric ANOVA followed by Dunn's multiple comparisons tests to detect significant differences among the three sites.

Results

Juvenile coral densities

Densities of juveniles measured with the 1-m^2 quadrat sampling method were generally low (<1 to 4 m^{-2}) and differed significantly among sites (Fig. 2A, Kruskal-Wallis $P = <0.001$). Post-hoc pairwise comparisons indicated similar densities (<1 m^{-2}, $P > 0.05$, Fig. 2A) at the Triumph and East Bache sites. Intermediate densities (1 to 2 m^{-2}) were observed at Alina's, Pacific, and Ball Buoy reefs while significantly higher densities (2 to 4 m^{-2}) were observed at the two southern patch reefs, Elkhorn and Isa's (Dunn's test groupings, Fig. 2A). Thus, the significant variation in juvenile density was between northern and southern reefs, not between offshore and patch reefs.

The proportions of total coral colonies that were juveniles also varied significantly among the seven sites (Fig. 2B). The sites with significantly higher proportions of juveniles (25–30%) were the two offshore bank reefs, Triumph and Pacific (due to low adult abundance), and the southern patch reefs, Elkhorn and Isa's (due to high
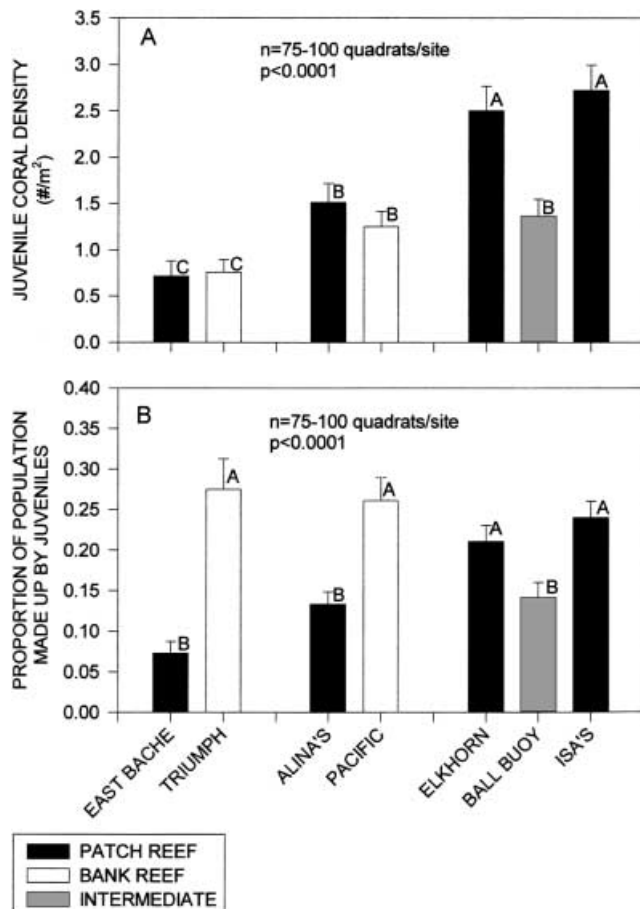
Fig. 2 Juvenile corals sampled in the belt transect sampling (mean ± 1 SE). **A** Density of juvenile colonies (no./m²). **B** Juveniles as a percent of total coral colonies at each site. *P*-values from Kruskal-Wallis one way nonparametric ANOVA. *Bars* in the same panel with the same letter do not differ significantly (Dunn's Test *P* > 0.05)

juvenile densities). The remaining sites (patch reefs: East Bache and Alina's and Ball Buoy) had juvenile proportions in the 5–15% range (Fig. 2B).

Juveniles of the massive broadcast spawner *Siderastrea siderea* were the most abundant on the offshore bank-barrier reefs (Triumph and Pacific), as well as on one of the patch reefs, East Bache. The brooding species *Porites astreoides* had the highest abundance of juveniles on the more southern Elkhorn, Alina's and Ball Buoy reefs.

Colony size frequency distributions

Chi-squared contingency table analyses indicated significant variation in the distribution of coral size classes among sites for all four species sampled (*P* < 0.001, Fig. 3). While most organisms, including corals, may be expected to have a size distribution dominated by small individuals, there is the expectation that the entire size range of a species will be represented in a population,
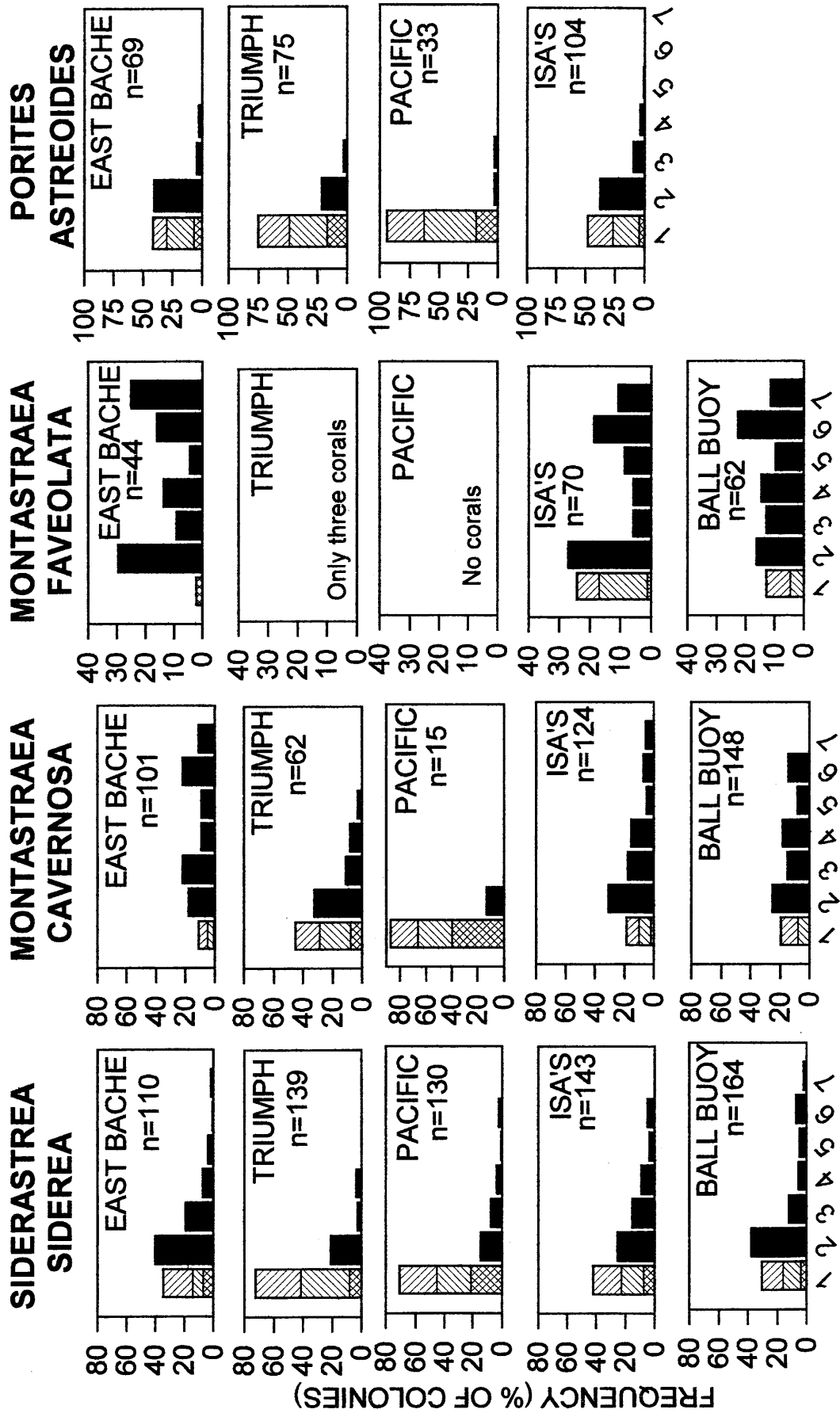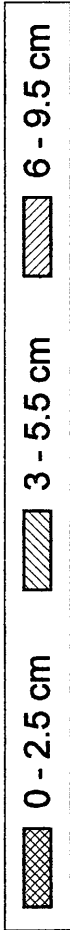
albeit with smaller numbers of older/larger individuals. However, the outer bank-barrier reefs, Pacific and Triumph, had truncated size distributions with 45–90% of populations in the smallest (< 10 cm) size class, and with a virtual absence of moderate to larger size classes of *Siderastrea siderea* and *Montastraea cavernosa* within the sampled areas (Fig. 3). No *M. faveolata* colonies were observed within the sampled plots at Pacific and only three colonies were encountered at Triumph. Coral abundances for other species were also depressed at these two sites, reflected in the small sample sizes for *Montastraea cavernosa* and *Porites astreoides* (Fig. 3). In contrast, the patch reefs East Bache and Isa's, along with the intermediate reef, Ball Buoy, had much more even size-class distributions with both small and large size classes well represented. These latter sites were also the only ones where sufficient numbers of *M. faveolata* were encountered to estimate a size frequency distribution.

Recruitment quadrats

The densities of juveniles observed in the smaller permanent quadrats (0.025 m², Fig. 4) were much higher than those measured in the larger quadrats (Fig. 2A). We attribute this to differing search methods and intensity, and possibly also to the different substrate topography examined in the two methods. In the initial census of the recruitment quadrats, the standing stocks of juvenile corals did not differ significantly among the three sites (Fig. 4, Kruskal-Wallis ANOVA *P* = 0.46). Nor did the annual mortality rates [mean (SE) of 29.5(12.0)% for East Bache, 21.8(8.8)% at Triumph, and 49.4(13.7)% at Ball Buoy; Kruskal-Wallis *P* = 0.2908]. However, the number of colonies recruiting into the quadrats at these sites during the 1-year interval differed significantly among sites (Kruskal-Wallace *P* = 0.019). During this period, recruitment at East Bache was significantly higher than at Triumph (Dunn's test *P* < 0.05) while Ball Buoy had an intermediate level of recruitment (Fig. 4). Even when one outlying quadrat at East Bache (in which 26 new recruits appeared during the 1-year interval) is excluded, the mean density of new arrivals at East Bache is still 7.1/m² and the Kruskal-Wallis non-parametric ANOVA still indicates significant variation in new arrivals among the sites. (None of the pair-wise comparisons is significant in this instance.)

Newly settled corals (single polyps) are not visible underwater, even when using this intensive search

▶

Fig. 3 Size frequency distributions of four coral species at five sites (based on measurements along the longest diameter of the colony). Size categories: *1* = 0–9.5 cm, *2* = 10–19.5 cm, *3* = 20–29.5 cm, *4* = 30–39.5 cm, *5* = 40–49.5 cm, *6* = 50–100 cm, *7* = >100 cm. The smallest size category (0–9.5 cm) is partitioned into smaller intervals represented by *hatching*, *n* equals number of colonies measured. Note different y-axis ranges for different coral species
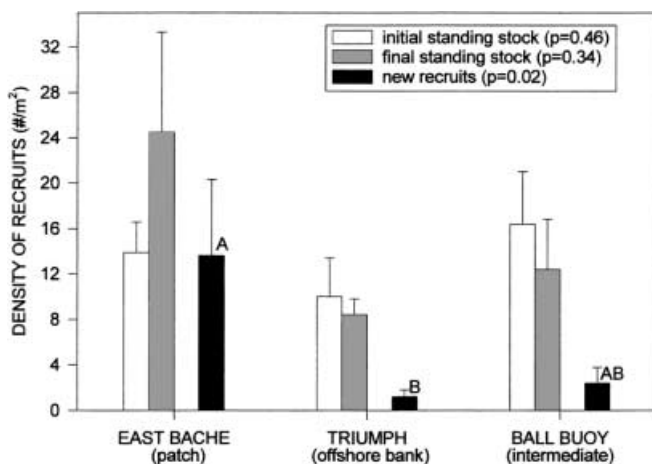
SIDERASTREA SIDEREA — MONTASTRAEA CAVERNOSA — MONTASTRAEA FAVEOLATA — PORITES ASTREOIDES

FREQUENCY (% OF COLONIES)

SIZE CATEGORY

Legend: 0 - 2.5 cm 3 - 5.5 cm 6 - 9.5 cm

Fig. 4 Mean (±1 SE) density of juvenile standing stock at initial census, density at final census, and new recruits arriving during the 1-year interval between censuses of the permanent quadrats at three reefs. *P*-values from Kruskal-Wallis one way nonparametric ANOVAs. For the new recruits, *bars* with the same letter do not differ significantly (Dunn's post-hoc test, *P* > 0.05). Note that at East Bache, the high mean recruitment and resulting higher densities at the second census are due to one anomalously high quadrat. If this outlying quadrat is excluded, the mean (SE) for new recruits drops to 7.1 (2.1) and the final standing stock drops to 16.6 (4.2)

method. However, we were able to identify very small juveniles (down to 1 mm diameter). Thus, although we cannot be sure that the new juveniles that we identified in the second census were not present at the first census at a size less than 1 mm (below our threshold of visual detection), from laboratory work with settlers obtained from cultured spawn, we know that most colonies in the 1 mm size range are less than 1 year old.

Despite the significantly higher rate of new recruitment at East Bache, the standing stock of juveniles at the second census did not vary significantly among sites (Fig. 4, *P* = 0.34). Thus, the three sites examined showed no significant differences in standing stock of small juveniles at both the start and the end of the study.

The massive broadcast spawner, *Siderastrea siderea*, was the most common species of new recruit at East Bache contributing approximately half of all new arrivals (Table 2). Brooders such as *Porites astreoides* and *Agaricia agaricites* were the most abundant new recruits at Triumph (Table 2) while Ball Buoy had approximately equal proportions of broadcast spawners (*S. siderea*), brooders (*Porites astreoides* and *Favia fragum*) and the hydrocoral *Millepora* spp. in the pool of new arrivals.

Discussion

Recruitment success

Neither of two different methods of assessing total juvenile coral abundance, (large quadrat sampling along transects of juveniles 0.5- to 5-cm diameter, and intensive

Table 2 Turnover of recruits in the 0.25 m² permanent quadrats (*n* = 15 for East Bache and *n* = 10 for Triumph and Ball Buoy) by species listed in approximate order of decreasing abundance. *RM* indicates the reproductive mode for each species, *S* broadcast spawners, *B* brooders, *U* unknown reproductive mode. *Initial* indicates mean density of recruits (1 mm to 2 cm diameter) present in the initial census in fall 1994. At the second census in fall 1995, these initial densities were partitioned into *Surviving* (relocated alive at the final census, given in no. colonies/ m²) and *Dead* (missing in the final census, given as % of initial). *New* indicates mean density of recruits arriving during the 1-year interval (i.e., present in the final but not the initial census). *Overall mortality* indicates mean (SE) percent for all species in all quadrats at each site

	RM	East Bache				Triumph				Ball Buoy			
		Initial no./m²	Surviving no./m²	Dead %	New no./m²	Initial no./m²	Surviving no./m²	Dead %	New no./m²	Initial no./m²	Surviving no./m²	Dead %	New no./m²
Siderastrea siderea	S	3.20	2.1	33	8.8	2.4	1.6	33	0.0	0.8	0.4	50	1.2
Porites astreoides	B	3.7	2.7	29	3.2	2.8	2.4	14	0.4	5.2	3.6	31	0.4
Agaricia agaricites	B	0.3	0.0	100	1.6	3.6	2.4	33	0.8	3.2	2.4	25	0.0
Favia fragum	B	1.1	0.5	50	0.3	0.8	0.8	0	0.0	3.6	2.8	22	0.8
Porites porites	B	0.0	0.0	–	0.0	0.4	0.0	100	0.4	0.8	0.8	0	0.8
Dichocoenia stockesii	U	0.3	0.0	100	0.0	0.0	0.0	–	0.0	0.0	0.0	–	0.0
Mycetophyllia spp.	B	0.3	0.3	0	0.5	0.0	0.0	–	0.0	0.0	0.0	–	0.0
Montastraea faveolata	S	0.3	0.3	–	0.0	0.0	0.0	–	0.0	0.4	0.4	0	0.0
Leptoseris cucullata	U	0.0	0.0	–	0.0	0.0	0.0	–	0.0	0.4	0.4	0	0.0
Eusmilia fastigiata	U	0.0	0.0	–	0.8	0.0	0.0	–	0.0	0.0	0.0	–	0.0
Millepora spp.	U	1.0	1.0	0	0.0	0.0	0.0	–	0.0	0.0	0.0	–	0.0
Total (no./m²)		10.1	6.9		15.2	10.0	7.2		1.6	14.4	10.8		1.2
Overall mortality				30 (12)				22 (9)				49 (14)	4.4

observation of 0.1- to 2-cm juveniles in small permanent quadrats) show any consistent differences in juvenile coral densities between coral-poor offshore bank reefs and nearby lagoonal patch reefs characterized by higher abundance of larger size classes of corals (Figs. 2, 4). There is still the possibility that larval settlement rates are lower on the offshore reefs, and in fact, we did observe significantly higher arrival of new recruits at East Bache than at Triumph Reef during the 1-year interval of observation of our permanent quadrats. However, other studies have reported great inter-annual variation in coral settlement rates (e.g. Wallace 1985; Miller and Hay 1996; Hughes et al. 1999), and reversal from one year to the next in the rank order of recruitment at compared sites (Wallace 1985). In our study, there was greater inter-annual variation in juvenile standing stock at East Bache than there was inter-site variation between East Bache and Triumph in the initial surveys (Fig. 4). Thus, we do not think that these limited recruitment rate data are reliable indicators of actual spatial differences in settlement/recruitment rates, and are insufficient support for the hypothesis that differential larval settlement is the cause of differences in coral population abundance and size structure between sites.

Methodological considerations

Corals at the early stages of recruitment are very small and difficult to see, especially in high relief areas with a high cover of encrusting organisms. Thus, obtaining accurate estimates of in situ coral settlement and recruitment rates is difficult. One common approach is to use artificial settlement plates which can be removed from the reef for microscopic examination (e.g. Rogers et al. 1984; Smith 1992; Tougas, pers. comm.). However, using artificial substrates has the potential disadvantage of depriving larvae of important, though poorly understood, chemical or physical cues for settlement (Morse et al. 1998). Thus, while this approach may give useful information on relative recruitment-poor levels of non-selective settlers between sites, it may underestimate the actual number of corals recruiting to a given area, and result in inexplicable variability. For example, a previous settlement plate study in BNP yielded very low estimates of recruitment (Tougas, pers. comm.), while Smith (1997) found extremely high densities of corals on artificial tiles at Conch Reef, in the Key Largo National Marine Sanctuary just south of BNP. In the current study, we chose several alternative approaches (with different limitations) in order to assess recruitment on natural reef substrates in BNP. The different methods we used (large [1 m^2] quadrat sampling, small [0.25 m^2] permanent quadrats, population size frequency distribution) yielded substantially different pictures of coral recruitment.

Coral recruitment estimates generated by studies using large (1 m^2) quadrats appear to greatly underestimate the actual abundance of very small coral colonies.

Our values for juvenile coral density generated from transect sampling at the 1 m^2 quadrat scale (Fig. 2A) are in the range of 1.2–3.4 juveniles m^{-2} and comparable to those reported by Chiappone and Sullivan (1996) for reefs further south in the Florida Keys.

However, our juvenile density estimates from smaller 0.25 m^2 quadrats that we placed preferentially on flat, clear substrate and examined with a more intensive search strategy were up to an order of magnitude higher than those we generated with visual surveys of the larger quadrats (Fig. 4), and were also slightly higher than those reported by Edmunds et al. (1998) using similar visual surveys of 0.25 m^2 quadrats for reefs in the Key Largo area of the Florida Keys. Therefore, contrary to other reports (Porter and Meier 1992; Tougas pers. comm.) that state that few or no corals are recruiting to BNP reefs, we found relatively high numbers of small corals on many of these reefs (Fig. 4), including large numbers of the broadcast-spawning, framework-building *Siderastrea siderea*. Porter and Meier (1992) used photographic monitoring of permanent quadrats while Tougas' study (pers. comm.) used artificial settlement plates, and the combination of these differences in methodology (artificial vs in situ natural substrates, photographic vs in situ examination) appears to have significant influence on recruitment rate estimates. In a study at Conch Reef in the Florida keys, Smith (1997) used both artificial settlement tiles and photographic monitoring of permanent in situ quadrats and reported an order of magnitude greater density of arrivals on the artificial settlement tiles than on the permanent quadrats in a 1-year interval. Edmunds et al. (1998) found consistently higher numbers of juvenile corals using visual methods in 0.25 m^2 quadrats than with close-up photography of smaller areas, and recommended visual methods as the most representative.

Overall, the high inter-annual variation in coral recruitment rate discussed above makes any estimate of coral recruitment rate based on only 1 or a few years of data of limited value. Thus, for purposes of understanding coral population dynamics, we propose that careful determinations of the standing stocks of juveniles provide a more interpretable indicator of recruitment "success" of a coral community than short-term estimates of recruitment rate. However, if one wants to obtain an accurate estimate of in situ recruitment rates, we suggest that an intense (and necessarily time-consuming) in situ search strategy is necessary, since photoquadrat (Porter and Meier 1992; Smith 1997) and larger scale in situ sampling methods (Chiappone and Sullivan 1996; this study Fig. 2A) appear to drastically underestimate recruitment rates (Fig. 4).

Post-settlement mortality

Although the offshore bank reefs (Triumph and Pacific) have similar densities of small juveniles to their adjacent patch reefs (Figs. 2A, 4), the coral size-frequency

distributions for four scleractinian species indicates that they have qualitatively different population structures, with large colonies being essentially absent (Fig. 3). Differences in growth rate could potentially result in two populations of the same age structure having different size frequencies, but several studies have found no difference in growth rates (for adult corals) between colonies on offshore and patch reefs of BNP and Key Largo area (Hudson 1981, 1994), although there was much temporal variability in growth rates for all sites. Therefore, there is no a priori reason to expect that the juvenile corals of the offshore reefs were growing slower than those of the patch reefs. This suggests that juvenile coral mortality is higher on the offshore reefs since the juvenile colonies are present but they do not seem capable of reaching larger size classes. There are several possible factors that could be responsible for higher juvenile coral mortality on the offshore reefs.

One primary agent of mortality in many populations is predation. Invertebrate predation on corals is well-known but, except for the cases of *Acanthaster* on Indo-Pacific reefs, and *Coralliophila* on Atlantic-Caribbean reefs, remains poorly studied (Glynn 1990; Carpenter 1997). There are conflicting results regarding the amount of damage inflicted on Caribbean reef corals by herbivorous fishes (Hixon 1997). Miller and Hay (1998) and Grotolli-Everett and Wellington (1997) both showed dramatic rates of predation on coral transplants on offshore bank reefs in the Florida Keys. In conjunction with the present study, a preliminary, unreplicated experiment conducted only at East Bache and Triumph reefs recorded significantly higher fish predation on juvenile coral transplants at Triumph than at East Bache (Miller et al. unpubl. data). This is a pattern consistent with the suggested hypothesis that juvenile mortality is higher on offshore bank reefs than patch reefs.

It is also possible that physical stresses are higher offshore and induce high rates of mortality. A feature of the spatial pattern in juvenile density found in the current study is the significantly greater coral densities on reefs in the southern region of the Park (Fig. 2A). The southern region of Biscayne National Park borders on John Pennekamp Coral Reef State Park and the Florida Keys National Marine Sanctuary, and these southern BNP reefs are more typical of reefs found in the 'richer' parts of the Florida reef tract (e.g. Key Largo; Jaap 1984). Burns (1985) suggested that both cold water and sediments associated with out-flux of Biscayne Bay waters from the north was limiting to shallow reef corals in Biscayne National Park, especially at Triumph Reef. However, companion measurements of temperature and sedimentation regimes in the current study sites show no differences between patch and bank reefs in rate of sediment deposition and suggest the temperature regimes are more extreme at the patch reefs than on the offshore bank reefs (Table 1, Weil et al. unpub. data).

Thus, while physical stress may help explain higher mortality at the northern versus southern sites, parameters measured in conjunction with the current study do not clearly correlate with differences between coral communities in offshore bank and patch reefs. For example, physical abrasion by coarse sediments during the frequent and prolonged storm fronts that traverse the area could help explain greater juvenile mortality on the offshore reefs. A more recent study (Szmant et al. in prep.) has documented that offshore resuspended sediments are coarser than those of more inshore areas, and a larger, coarser particle size is potentially indicative of greater abrasion stress on the offshore reefs. Eutrophication and sedimentation stress have also been shown to increase juvenile coral mortality, and to affect some species of coral more than others (Wittenberg and Hunte 1992). However, if any eutrophication is present within the reef areas of BNP, it would be greater nearshore than offshore (Szmant and Forrester 1996), and total sedimentation rates were also higher at the patch reefs than they were offshore (Table 1 and Szmant et al. in prep.). Whatever the specific cause(s) of higher juvenile coral mortality offshore, it is intuitively obvious that they have been acting for centuries or millenia, since the geological record shows consistently low rates of coral-derived carbonate accumulation on the offshore linear bank reefs of this region of the Florida Keys (Shinn et al. 1977; Shinn 1988).

Physical structure and architectural complexity (created by large corals) are reef characteristics long recognized to influence reef biota. The greater structural complexity of patch reefs provided by large corals may contribute to greater juvenile coral survival by providing more nooks and crannies in which vulnerable coral juveniles might escape detection by visually oriented grazing fishes and/or escape stress or mortality from physical disturbances (e.g., sand scour and other storm disturbances), hence yielding further development of the physical structure. McCook (1997) in his study of zonation in macroalgal standing stock on reefs in the central Great Barrier Reef postulates similar feedback mechanisms involving coral recruitment and development of habitat structure that affect grazing rates and physical stresses such as sediment accumulation. Such mechanisms, by fostering or precluding the development of physical structure, may have broad implications for reef trophodynamics, nutrient cycling, and ecosystem function (Szmant 1997).

In conclusion, we found little evidence to support the hypothesis that coral early recruitment processes are different between coral-poor offshore bank reefs and lagoonal patch reefs with greater coral cover, although we did find that coral recruit density does increase from north to south within the Park. In fact, at all sites, coral recruitment success as indicated by juvenile densities was substantially higher than has been previously reported for BNP. This lack of difference in recruitment success, coupled with large and obvious differences in coral cover and abundance of large colonies, suggests that high juvenile mortality on the offshore bank reefs, possibly caused by fish predation, physical stresses (e.g. abrasion during storms), and/or historical events such as winter

cold snaps, is the primary factor responsible for observed differences in coral community structure between these two types of reef in BNP.

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