

FINAL REPORT

COOPERATIVE AGREEMENT NO. CA5280-4-9001

**ASSESSMENT OF HURRICANE ANDREW EFFECTS
ON BNP REEF CORALS**

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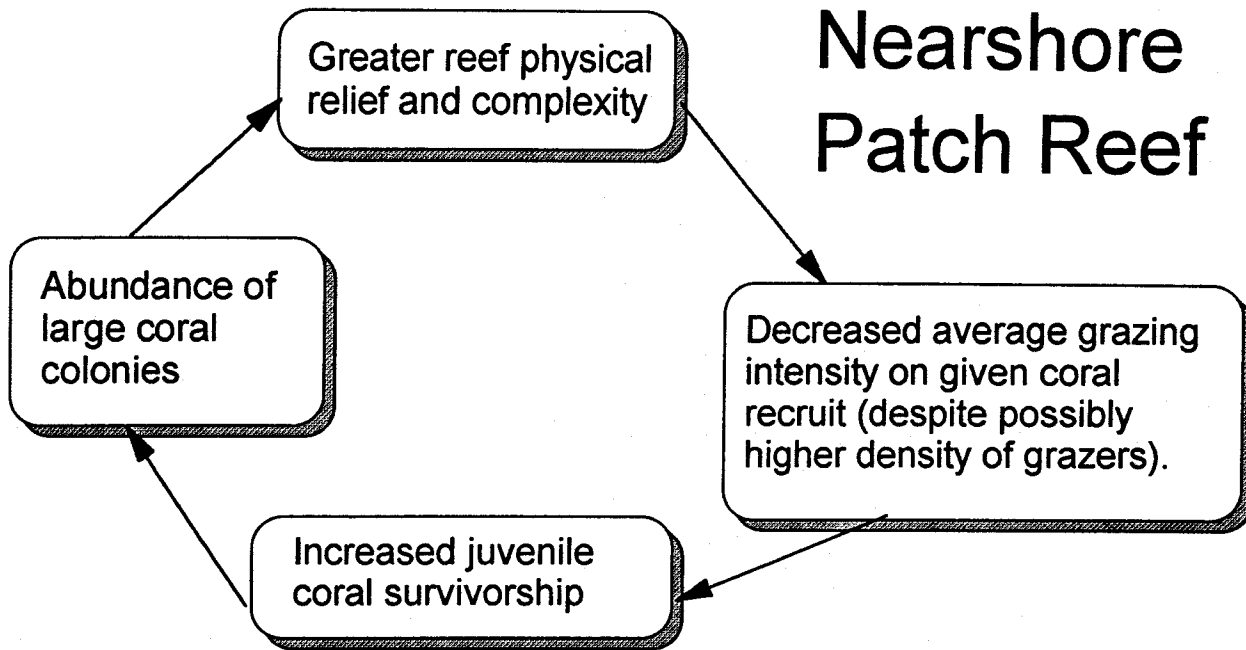
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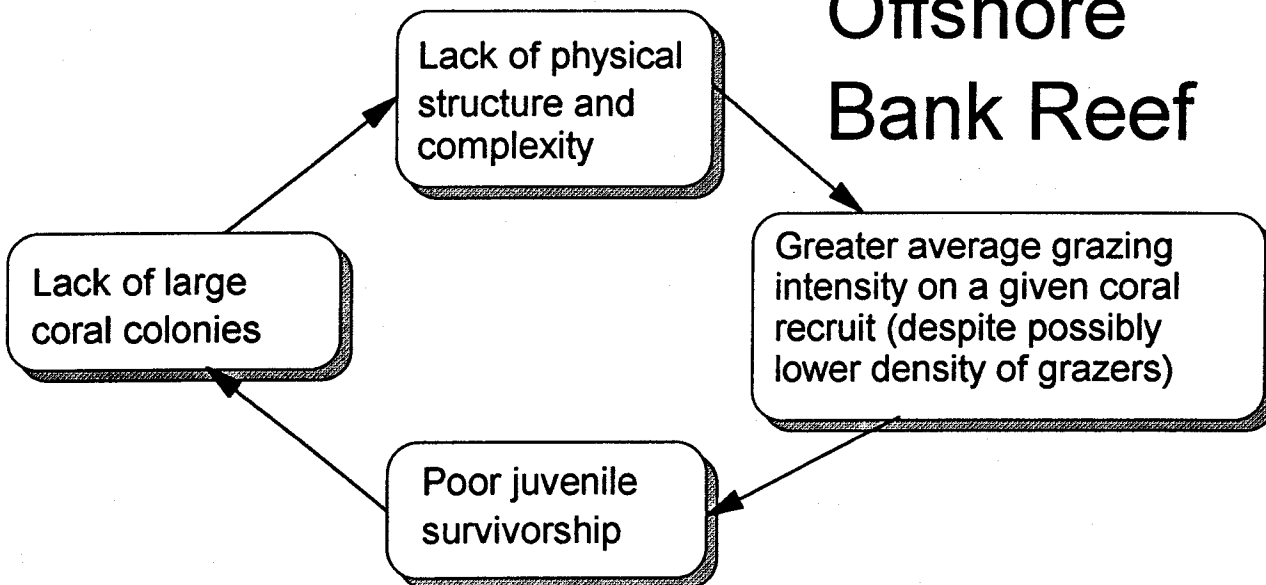
The United States Department of the Interior
National Park Service
Biscayne National Park
Homestead Florida

18 June, 1997

Nearshore Patch Reef



Offshore Bank Reef



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EXECUTIVE SUMMARY

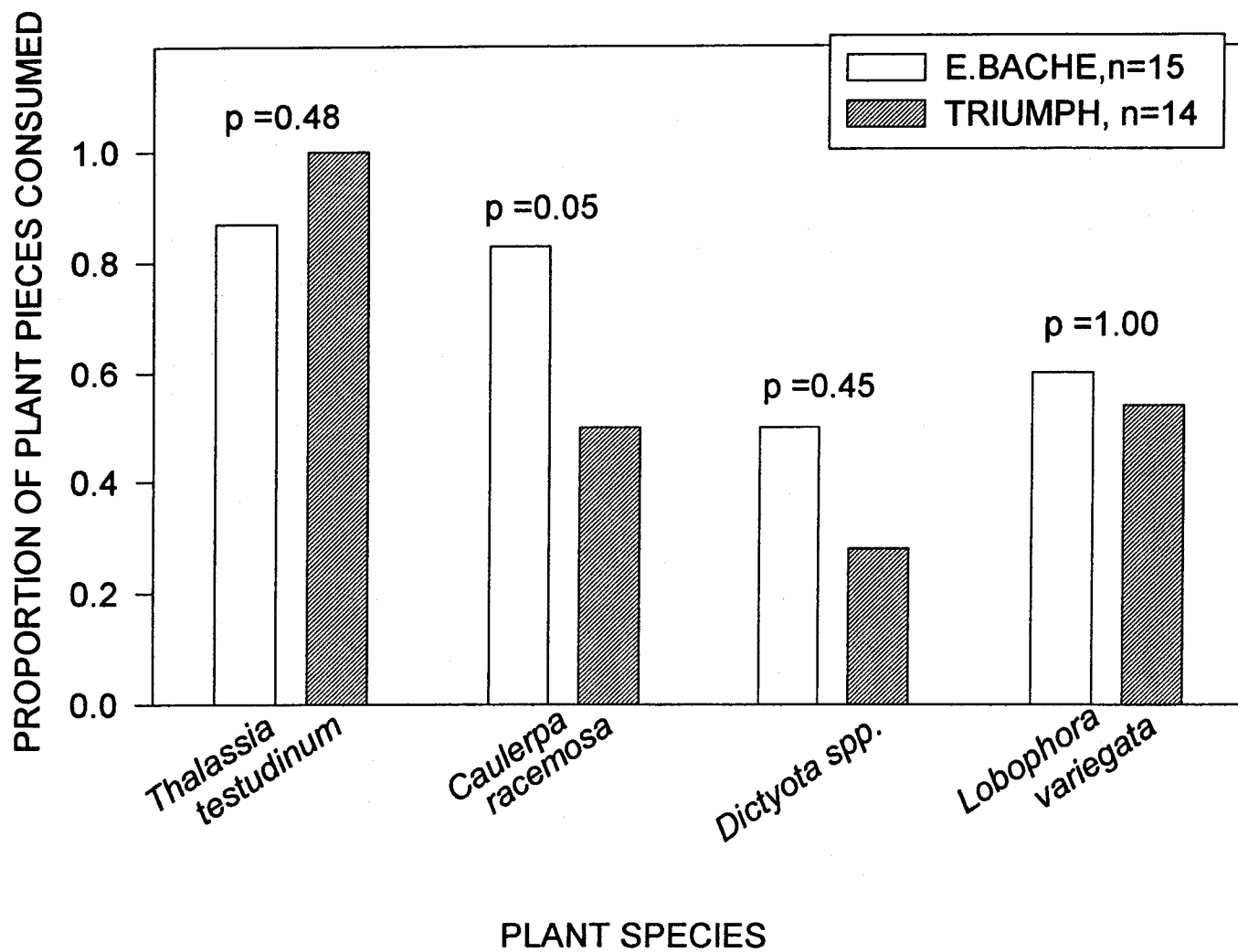
This is the final report for Cooperative Agreement No. CA5280-4-9001, "Assessment of Hurricane Andrew Effects on BNP Reef Corals". An extensive report, which included descriptions, tables and graphs of all of the various types of data collected in this study, was provided in the Fifth Biannual Report, dated June 1, 1996. This final report includes an executive summary of the major findings of the study, a copy of a manuscript based on the work that has been submitted for publication ["Recruitment patterns and grazing regime as factors structuring reef benthic communities in Biscayne National Park, USA.", by M.W. Miller, E. Weil and A.M. Szmant, submitted to Marine Ecology Progress Series, April 1997], and meta-data documentation of the data disks that include all of the raw and intermediate data sets generated by the study. A complete set of the data is included on 3.5" floppy diskettes. Additional manuscripts are in preparation for submission to peer reviewed journals, and will be provide to NPS as they become available. All publications will acknowledge this contract and other supported received from BNP for the project.

SUMMARY OF PROJECT COMPONENTS.

The work executed under this agreement was organized into 7 tasks [Task 1: Quantitative Description of the Benthic Community Structure of Nine Reef Localities; Task 2: Monitoring Coral Recruitment on Reefs; Task 3: Monitoring Hurricane-damaged Colonies; Task 4 : Coral Population Size-frequencies; Task 5 : Assessment of Spatial and Temporal Variability in Environmental Parameters; Task 6: Coral Reproductive Status; and Task 7 : Cage/transplant Experiment. The details of how each task was conducted were previously reported in Bi-Annual Report 5, and will not be repeated here.

PROJECT SUMMARY

The coral reefs of Biscayne National Park (BNP), Florida, lie at the northern fringe of the Florida Reef Tract and of coral reef distribution in the western Atlantic. Environmental forcing of community structure is expected to be strong at this latitude. Live cover, abundances and diversity of scleractinian corals, octocorals, sponges, zoanthids and hydrocorals as well as cover of algae and other substrate types were quantified for each of nine reef sites along nearshore/ offshore and north/south gradients within the Park. We also monitored environmental factors such as temperature, sedimentation, and nutrient content in



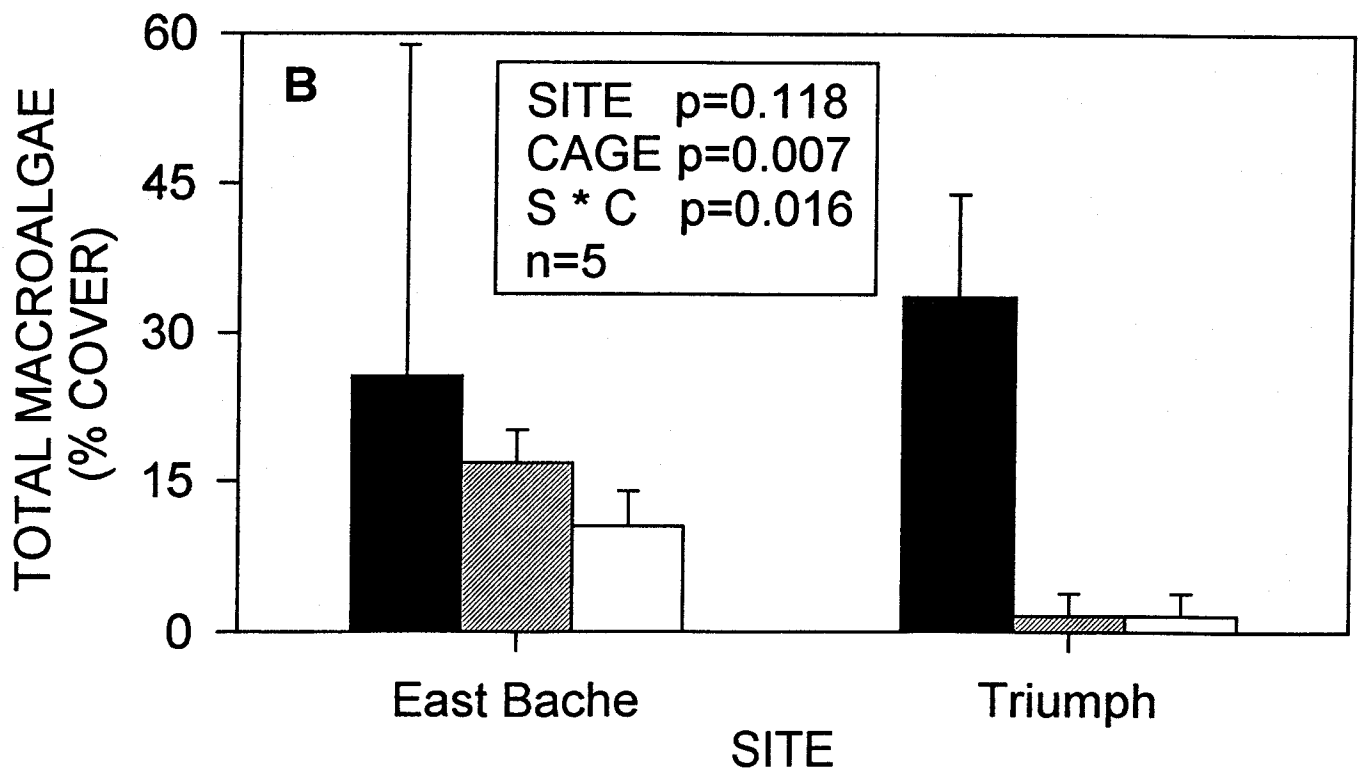
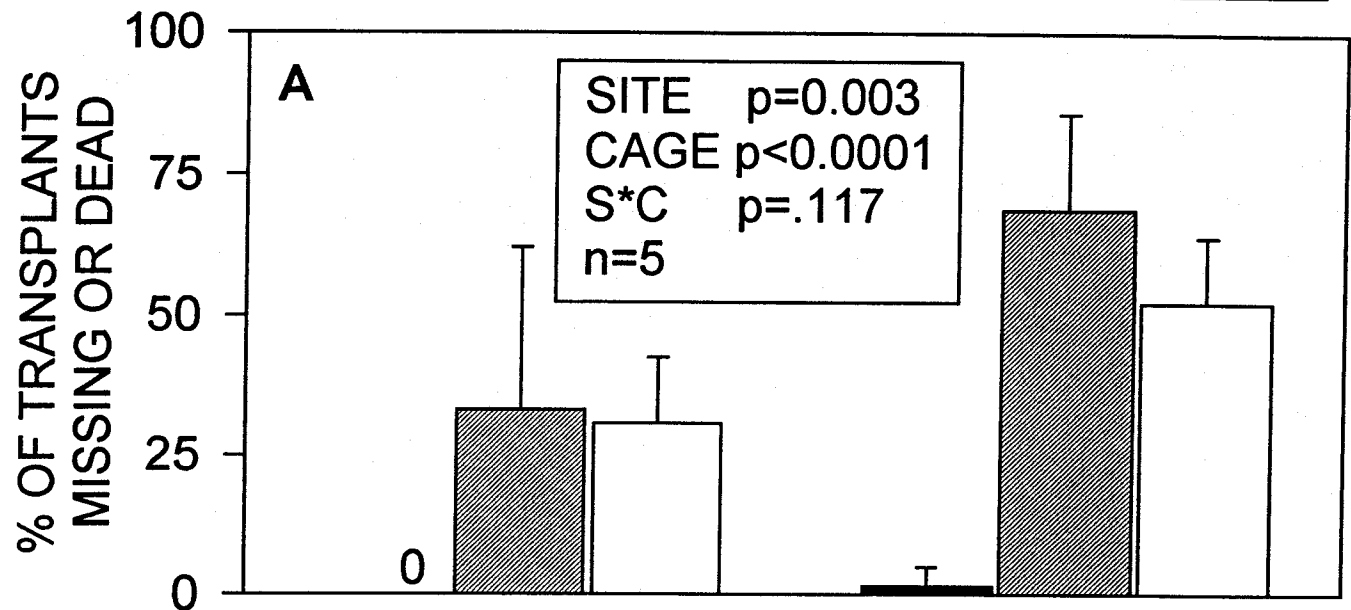
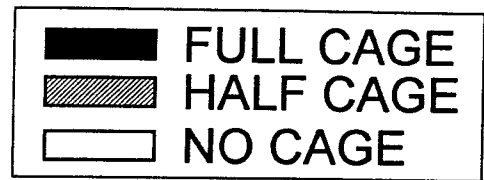
the sediment and water column at the same sites to examine the potential role of these factors in explaining spatial variation in benthic community structure.

The outer bank-barrier reefs of BNP were found to have more depauperate coral communities, with little relief and few large corals, than the mid-shore patch reefs, which support greater cover and richness of corals despite more stressful temperature regimes and greater proximity to hypothetically detrimental terrigenous and bay influences (see below). Nearshore patch reefs showed higher live cover, abundances and species richness of cnidarians and sponges, a greater abundance of large coral colonies and octocoral colonies, and reduced prevalence of bare substrate and algal turf than their adjacent offshore reefs (Table 1, Figure 1). In general, benthic community structure was mostly dominated by algal turf. Porifera was the most diverse group at both the species and genera level (66 spp. in 41 genera) compared to scleractinians (52 spp. in 23 genera) and octocorals (43 spp. in 11 genera, Table 1). Despite being less diverse, octocorals were the most abundant group in eight of the nine reefs sampled. *Madracis senaria*, a common, massive coral in the southern and western Caribbean, is a new record for Florida.

Both offshore and inshore sites showed a north/south gradient with significantly higher live cover (Figure 1), abundances and diversity of cnidarians and sponges and lesser cover of bare pavement and algal turf at the southernmost sites. Coral juvenile densities were positively and significantly correlated with adult densities. Juveniles of broadcast-spawning species were more abundant at both inshore and offshore sites (Table 2).

Temperature regimes were more variable and more stressful at nearshore than at offshore sites, a pattern opposite to what would be expected to correspond to the greater coral abundance at the nearshore sites. Overall levels of sediment deposition and water column nutrient concentrations were temporally variable, and more influenced by episodic events such as storms than by any spatial gradient. However, the quality of the sediments did vary spatially. Sediments deposited on nearshore reefs had significantly a higher proportion of finer particles, were significantly higher in total nitrogen content, and had higher N:P ratio than those deposited on offshore reefs. Sediment nitrogen content also decreased from north to south. These patterns of environmental factors provide no clear correlation with the observed spatial patterns of benthic community structure within the study area suggesting that other factors such as historical effects of severe cold snaps or other sources of juvenile coral mortality are the dominant structuring forces.

The role of recruitment limitation as a cause of the low hard coral abundance in the bank-barrier reef communities was assessed by examining 1) size-frequency distributions of coral populations, 2) recruitment to permanent quadrats (0.25 m²) on natural reef substrate, and 3) juvenile and adult coral densities. These data show that while recruitment is comparable between reef types, large coral colonies are virtually absent from the bank-barrier reefs. This suggests that juvenile survival, not recruitment rate, is limiting corals offshore. A



caging experiment showed that grazers (especially parrotfishes) imposed higher levels of mortality on coral juveniles at a bank-barrier site than at an adjacent patch reef. Grazer exclusion also resulted in a significantly higher degree of macroalgal proliferation at the bank-barrier reef. Thus, recruitment limitation does not appear to explain the impoverished coral communities on offshore bank reefs in BNP. Instead, high levels of juvenile coral mortality, including high grazing loss, appear to be the dominant factor structuring these communities.

CONCLUSIONS

1- Overall, the nearshore patch reefs and offshore bank reefs in BNP differ significantly in benthic community structure with the inshore reefs displaying quantitatively greater coral, octocoral and sponge cover and densities. These patch reefs also had larger coral colonies, particularly *Montastraea* spp. Of the offshore reefs, Ball Buoy is the only one with significant coral cover and with large stands of live *Acropora palmata*. The other offshore localities show very low cover of cnidarians and sponges and high cover of turf algae and crustose algae.

2- Live cover, density, and diversity of scleractinian corals, octocorals and sponges increase from north to south. Isa's reef had the highest diversity and density for these three groups. The Soldier Key site has a distinct biological community from the other sites. This site is mostly dominated by transient populations of fleshy algae over a fine sediment substrate with sparse colonies of octocorals and sponges.

2- Patterns of community composition do not correlate with measured variation in environmental factors such as temperature, sedimentation levels, or nutrient concentrations (sediment or water column). In fact, temperature regimes appear to be potentially more (not less) stressful on the inshore reefs.

3- Sedimentation rates are much more influenced by episodic events such as storms than by spatial gradients. Resuspended sediment nitrogen levels do show a spatial pattern with increased nitrogen levels in the inshore vs. offshore sediments.

4- Scleractinian and octocoral recruitment is high in most reefs. With the exception of Isa's reef in the south, the proportion of colonies that are juvenile (versus adult) is higher on the offshore reefs compared with the inshore reefs. Since the inshore reefs show higher densities of larger corals and octocorals, there appear to be greater rates of juvenile mortality on the offshore reefs.

5- The only measured environmental factor which did show a pattern congruent to the spatial patterns in community structure was grazing intensity. The caging experiment demonstrated significantly greater loss of coral juveniles due to grazing on an offshore versus an inshore reef.

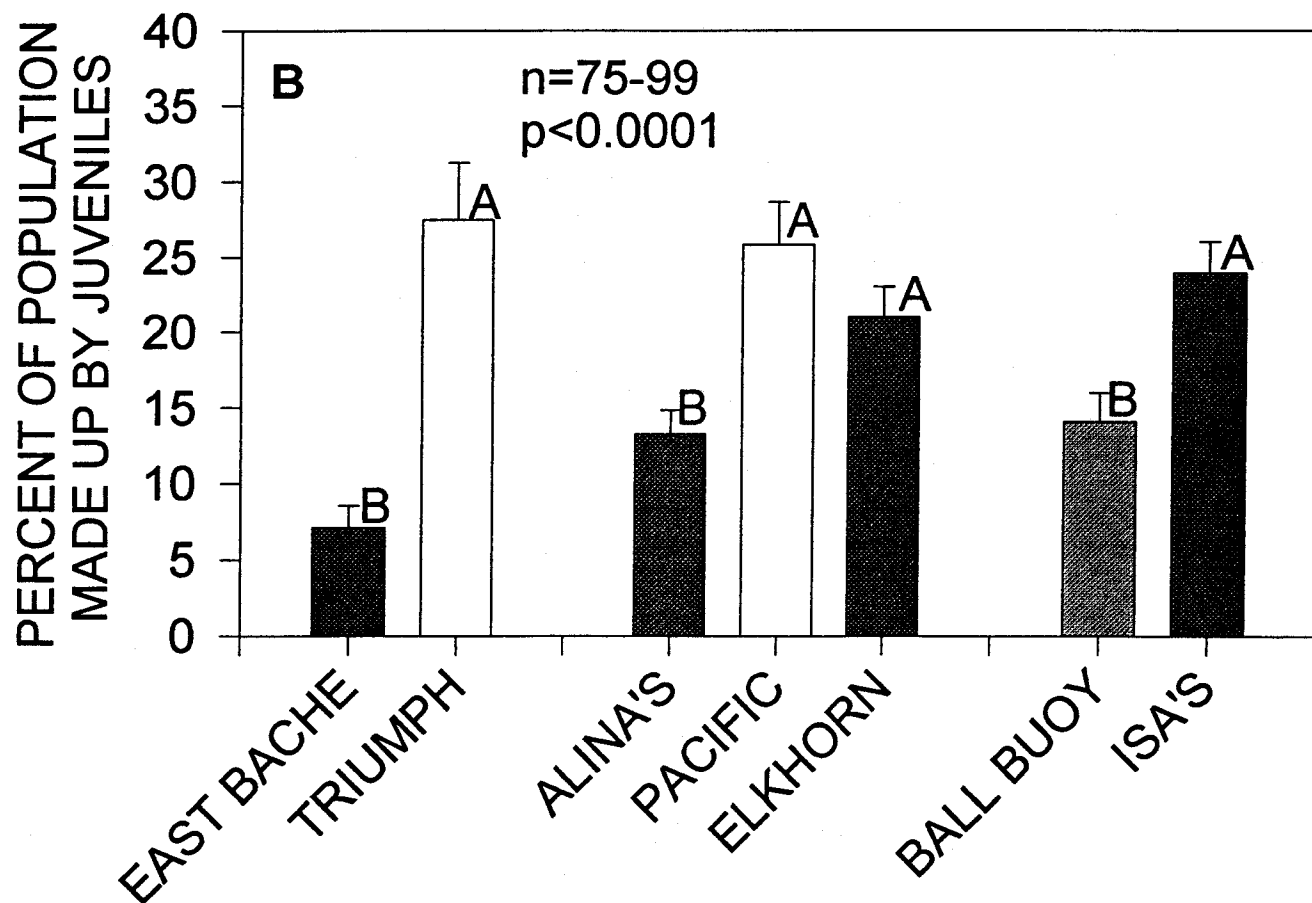
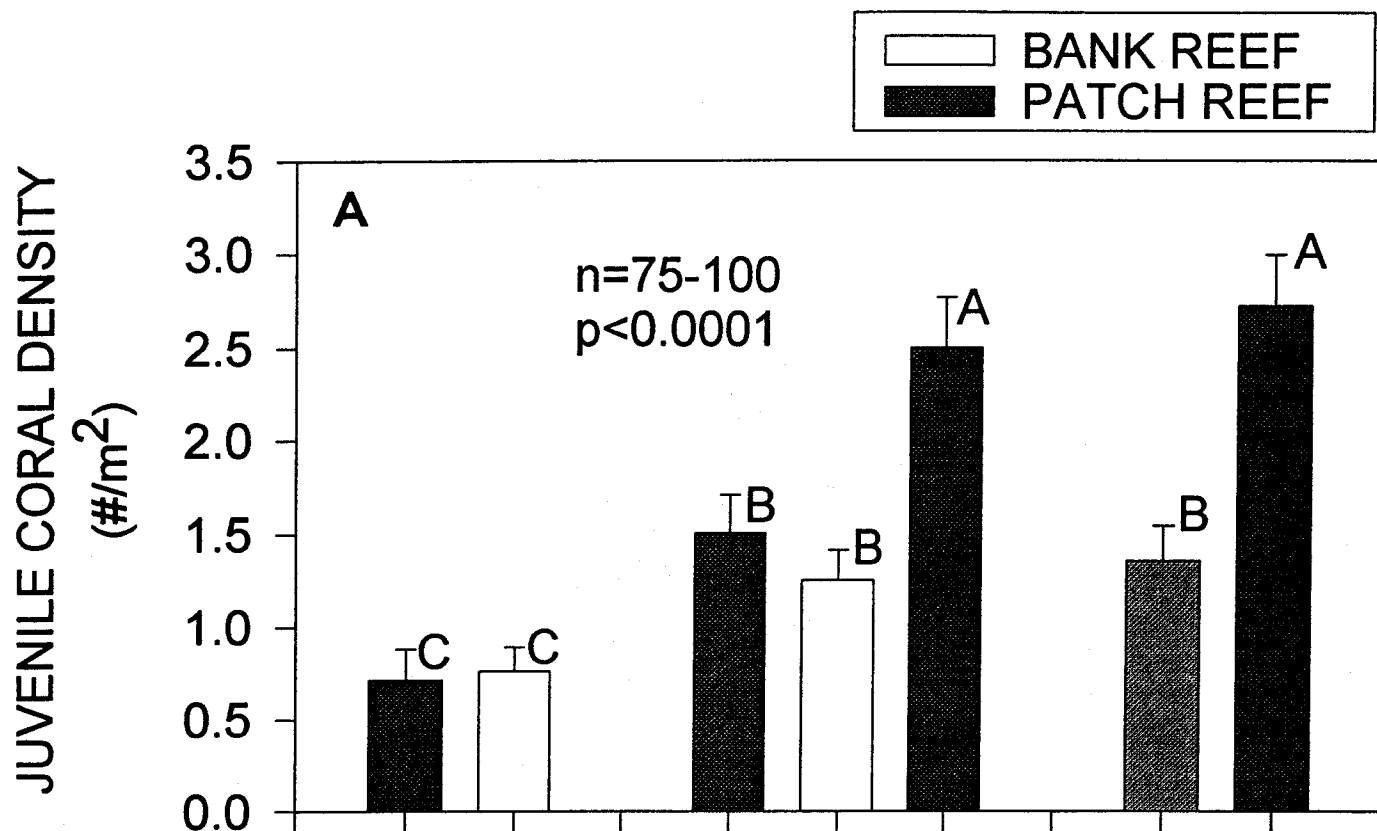


Table 1. Summary table of site and biotic characteristics of nine reefs sampled in Biscayne National Park.
Density is in colonies/m².

REEF SITE	FOWEY	SOLDIER	TRIUMPH	EBACHE	PACIFIC	ALINA'S	ELKHORN	BBUOY	ISA'S
Latitude (N)	25° 35.38	25° 35.25	25° 28.31	25° 28.98	25° 22.18	25°23.20	25° 21.78	25°18.52	25° 19.91
Longitude (W)	80° 05.69	80° 09.18	80° 06.72	80° 08.44	80° 08.36	80°09.77	80° 09.94	80° 11.99	80°11.87
Depth (m)	3-10	3.5-4.5	3-7	1-5	2-10	2-6	1-5	2-9	2-6
Reef type	relic-bank	relic-bank	relic-bank	patch	relic-bank	patch	patch	bank-barrier	patch
Number of transects	5	5	5	4	5	4	5	5	4
Number of quadrats	100	100	100	80	100	91	100	100	75
NUMBER OF SPECIES									
Hard Corals	28	12	24	40	30	39	29	40	43
Octocorals	28	23	32	40	29	39	34	39	41
Sponges	37	21	31	31	30	34	34	36	48
NUMBER OF GENERA									
Hard Corals	15	8	13	18	15	21	14	20	22
Octocorals	11	8	11	11	11	11	11	11	11
Sponges	25	16	21	23	19	25	23	29	35
PERCENT COVER									
Hard Corals	2.54	0.41	1.96	19.38	1.93	15.12	9.81	12.69	12.09
Octocorals	1.18	0.8	1.69	9.23	1.34	4.71	1.98	3.37	10.39
Sponges	5.04	2.34	2.22	5.43	1.02	4.34	2.31	4.85	11.83
Zoanthids	0.59	0	1.96	2.27	0.64	0.85	0.38	2.1	2.66
Hydrocorals	0.19	0.018	0.33	0.76	0.24	0.84	0.84	2.52	0.72
Fleshy Algae	67.37	74.96	73.03	45.8	61.28	58.68	63.88	40.87	28.66
Turf Algae									
Crustose Algae	11.12	0.84	8.76	10.3	14.3	5.88	5.49	15.59	11.08
Sand	8.74	19.72	8.76	1.59	7.59	4.73	6.31	10.86	15.76
Bare substrate	3.17	0	1.14	3.02	8.13	3.48	4.26	5.8	5.3
DENSITY									
Hard Corals	3.46	0.8	3.2	7.92	4.68	10.08	10.6	10.52	11.84
Octocorals	8.14	7.93	14.66	22.27	8.46	19.52	7.82	16.41	41.11
Sponges	5.36	3.77	3.84	8.68	3.29	8.77	4.84	8.04	21.25
Zoanthids	1.82	0	2.43	2.22	1.71	2.13	1.62	2.16	2.81
Hydrocorals	1.9	1.8	3.14	2.51	2.37	2.73	2.21	3.59	3.17

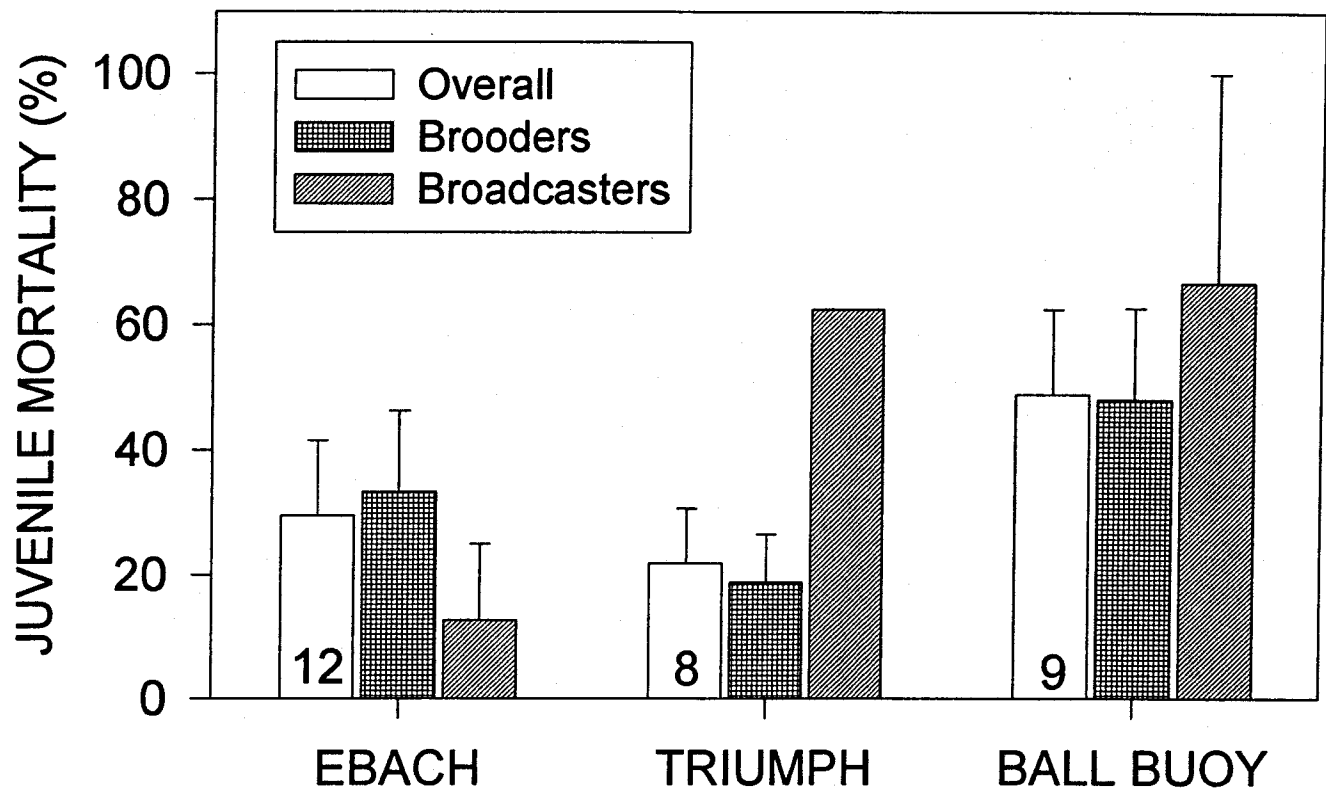
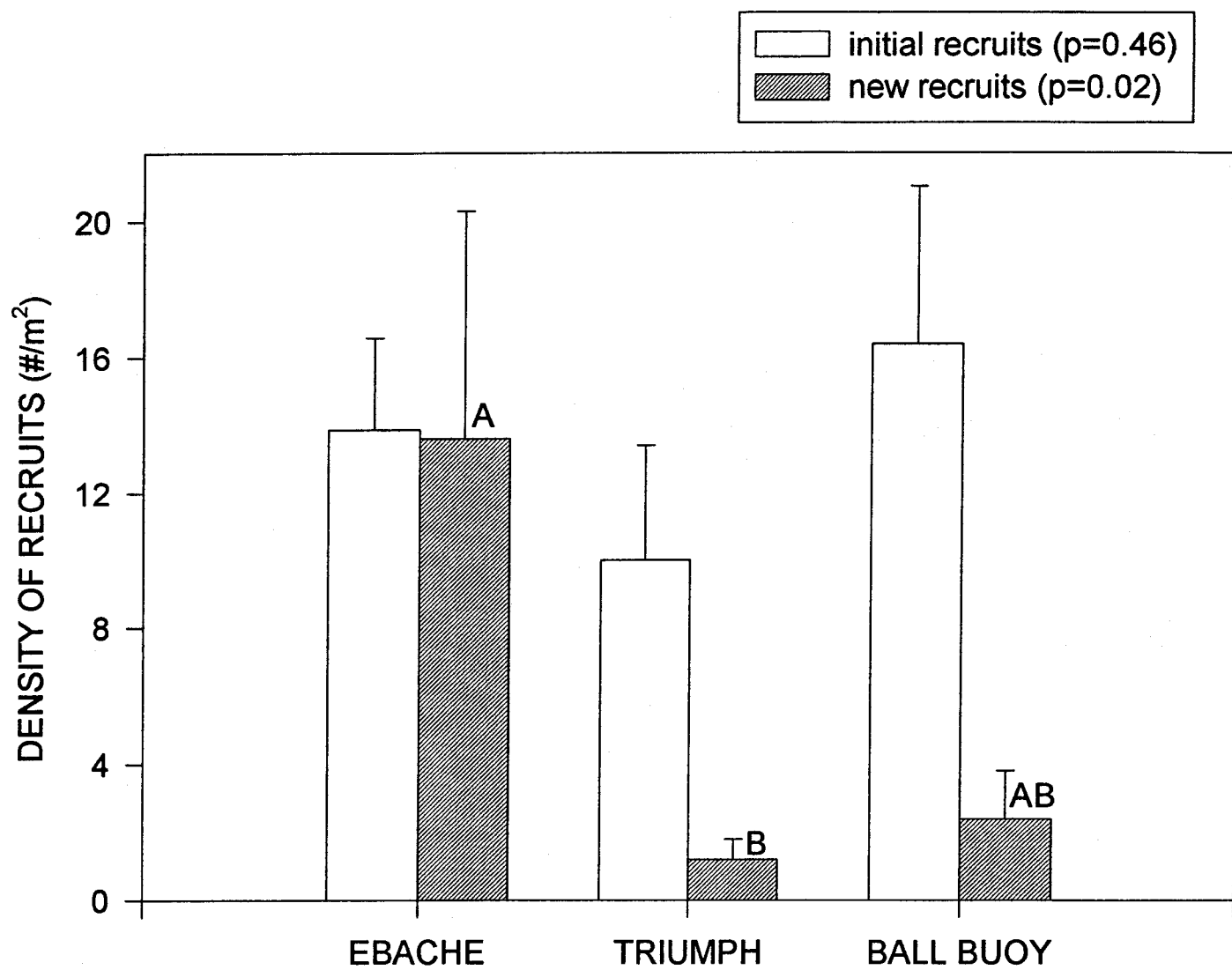
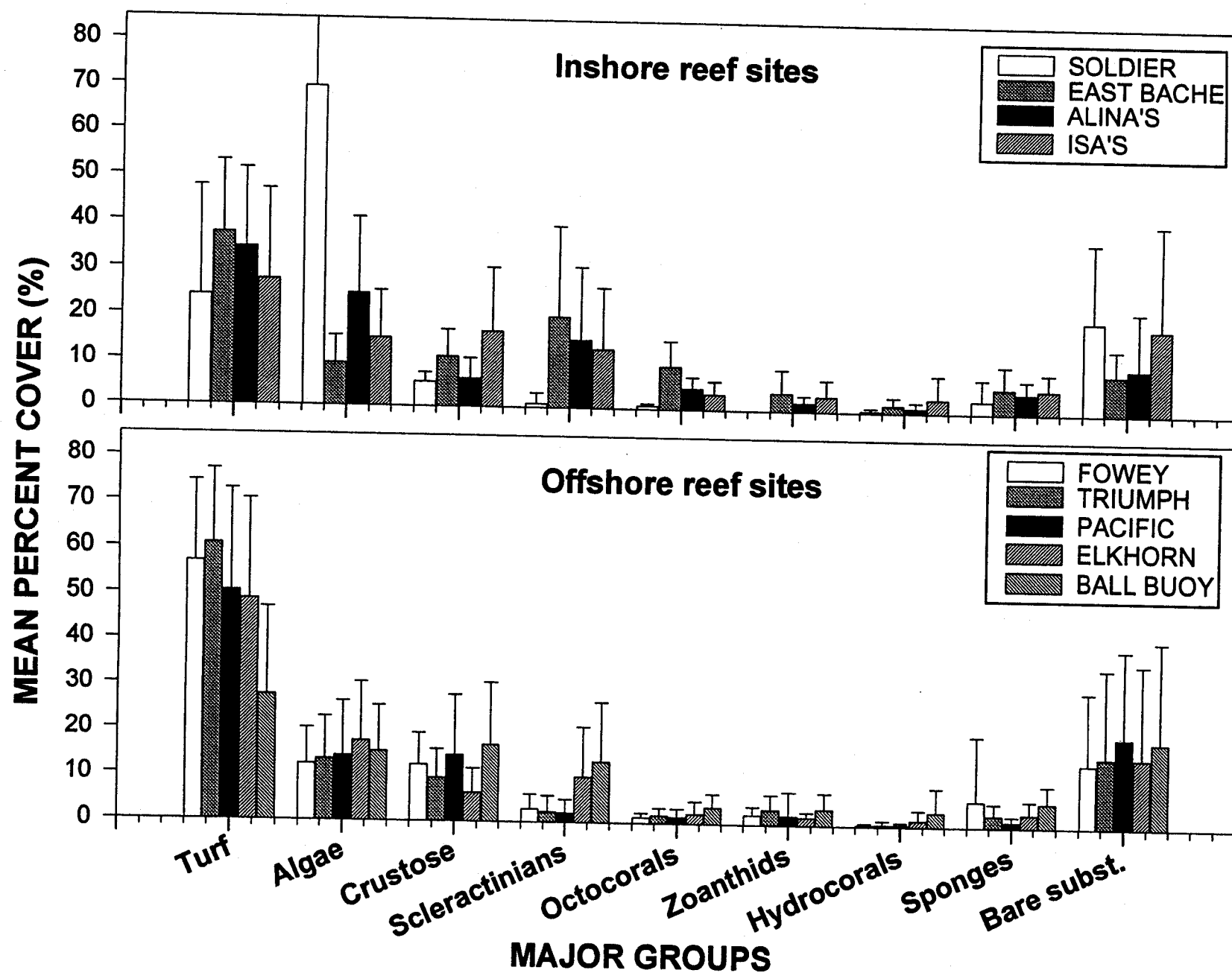
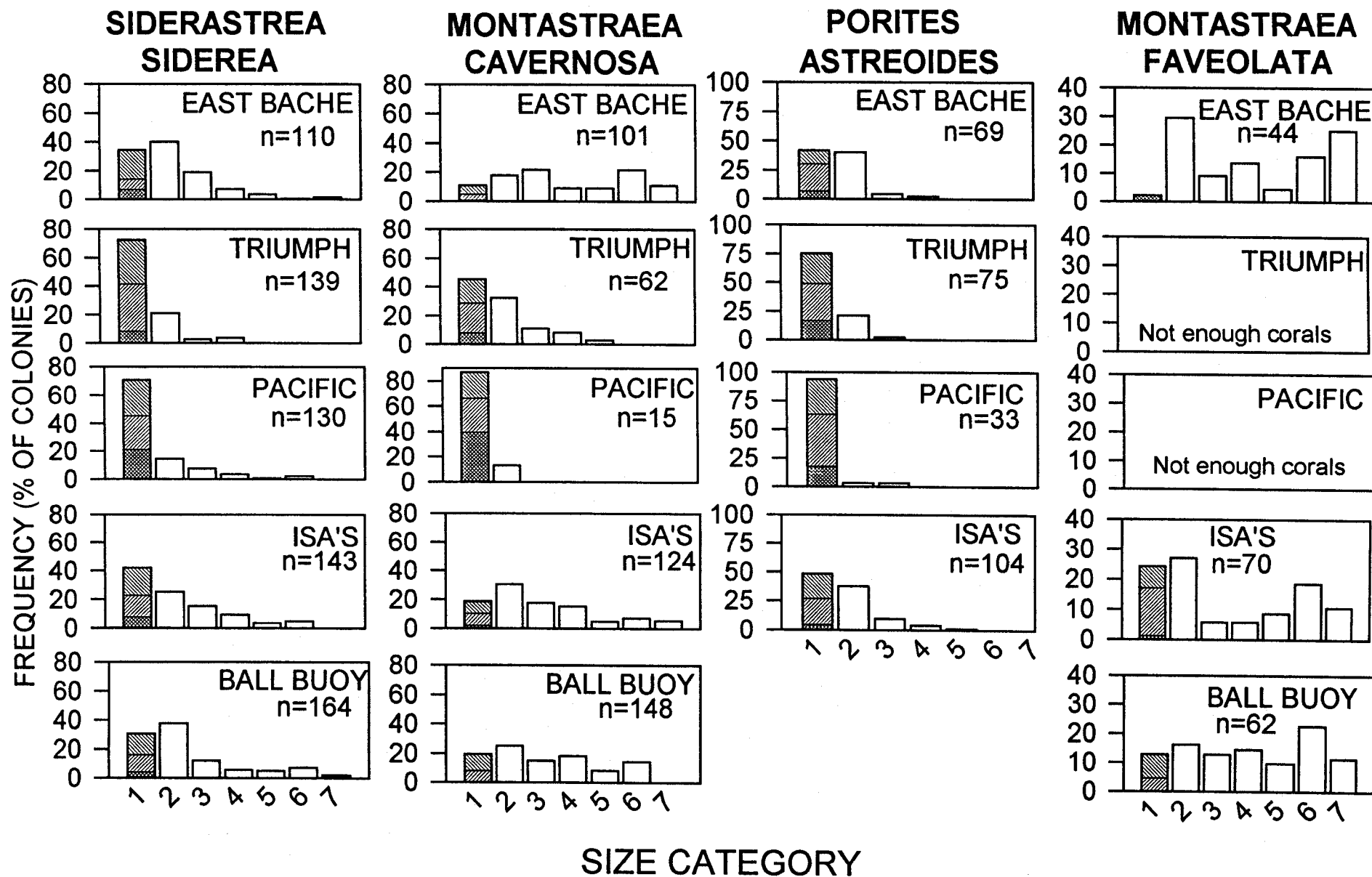
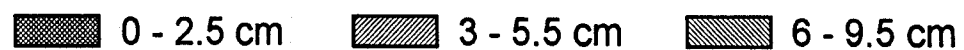


Table 2. Summary table for reproductive patterns and juvenile/adult densities (col/m²) in each reef site sampled in BNP. * = Hermaphrodite-broadcaster, ¹ = hermaphroditic brooder; ² = gonochoric broadcaster; ³ = gonochoric brooder; ⁴ = mixed pattern; ⁵ = unknown reproductive pattern and developmental mode. Total inshore and offshore numbers are the sum of juveniles and adult colonies in quadrats. P. astreoidesY and B are the two common color morphs (yellow-green and brown) and are considered as the same species. Total adult colonies and densities include all species of coral sampled in quadrats.

REEF SITES	FOWEY	SOLDIER	TRIUMPH	BACHE EAST	PACIFIC	ALINA'S	ELKHORN	BALL BUOY	ISA'S	Colonies Inshore	Colonies Offshore	Total
<i>Acropora cervicornis</i> °						.02/.11	.01/.01			2/11	1/1	3/12
<i>Acropora palmata</i> °						.02/.02				2/2	0	2/2
<i>Agaricia agarickes</i> °	.08/.62		.03/.67	.01/.20	.12/1.34		.02/.28	.05/2.25	.05/1.09	4/82	30/516	34/598
<i>Agaricia purpurea</i> *										1/16	0	1/16
<i>Agaricia tenuifolia</i> *						.01/.19				1/17	0	1/17
<i>Colpophyllia natans</i> *					.01/.01	.01/.01			.05/.01	5/2	1/1	6/3
<i>Dichocoenia stockesii</i> °	.05/.46	.01/0	.07/.17	.04/.14	.04/.04	.05/.22		.02/.27	.24/1.17	27/109	18/94	45/203
<i>Dichocoenia stellaris</i> °				.03/.01						2/11	0	2/11
<i>Diploria clivosa</i> °	.02/.10					.04/.09	.04/.28		.01/0	5/8	6/38	11/46
<i>Diploria labyrinthiformis</i> °	.04/.01				.03/.02	.03/.01		.04/.09	.03/.04	5/4	11/12	16/16
<i>Diploria strigosa</i> °					.02/.03	.04/.05	.03/.06	.02/.09	.04/.15	7/16	7/18	14/34
<i>Eusmilia fastigiata</i> °									.04/.05	2/4	0	2/4
<i>Favia fragum</i> ¹		.09/.11				.01/.33				10/41	0	10/41
<i>Madracis decactis</i> °					.01/.10					0	1/10	1/10
<i>Meandrina meandrites</i> °	.01/.12		.01/.08		.01/.05					0	3/25	3/25
<i>Meandrina memorialis</i> °					.01/.01					0	1/1	1/1
<i>Montastraea annularis</i> °			.01/0	.01/.14	.01/.01	.05/.26			.01/.04	7/38	2/1	9/39
<i>Montastraea cavernosa</i> °	.04/.06		.11/.12	.04/.31	.11/.01	.04/.24		.11/.50	.20/.23	22/74	37/69	59/143
<i>Montastraea faveolata</i> °	.02/.02				.01/0	.01/.38		.06/.14	.07/.28	6/46	6/16	15/62
<i>Montastraea franksi</i> °	.01/0			.03/.11	.04/.02			.01/.08	.03/.09	4/16	6/10	10/26
<i>Mycetophyllia aliciae</i> ¹				.01/.31					.07/.05	6/29	0	6/29
<i>Mycetophyllia danaana</i> *									.12/.20	9/15	0	9/15
<i>Mycetophyllia lamarckiana</i> *								.06/.14	.01/.04	1/3	6/14	7/17
<i>Portes astreoides</i> B ²	.06/.18		.09/.12	.20/.78	.02/0	.25/.55	.03/.08	.08/.11	.48/.65	161/75	28/49	103/210
<i>Portes astreoides</i> Y ²	.10/.11		.09/.10	.08/.33	.12/.12	.46/.63	1.87/3.03	.52/1.16	.23/.13	65/93	271/452	335/545
<i>Portes divaricata</i> ¹		.01/.04								1/4	0	1/4
<i>Portes portes</i> ²	.10/.27		.10/.34	.01/.38	.23/.85	.22/3.4	.45/3.14	.19/1.36		21/339	107/596	128/935
<i>Scolymia cubensis</i> °									.01/.33	1/25	0	1/25
<i>Siderastrea siderea</i> °	.21/.26	.31/.24	.24/.33	.26/.98	.41/.18	.20/.84	.04/.39	.21/.63	1.4/1.7	303/174	11/179	284/482
<i>Solenastrea boumomi</i> °		.01/0							.01/.07	5/2	0	2/5
<i>Solenastrea hyades</i> °		.01/0								1/0	0	1/0
<i>Stephanocoenia intersepta</i> °	.01/.03		.02/0		.05/.03				.05/.44	4/33	8/6	12/39
Juvenile colonies	75	44	77	57	125	136	249	137	235	472	663	1135
Juvenile density (col/m ²)	0.75	0.44	0.77	0.71	1.25	1.49	2.49	1.37	3.13	1.53	1.22	1.34
Adult colonies	224	39	193	294	282	668	727	682	506	1507	2108	3615
Adult density (col/m ²)	2.24	0.39	1.93	3.68	2.82	7.34	7.27	6.82	6.75	4.36	4.22	4.27
Number of quadrats	100	100	100	80	100	91	100	100	75	346	500	846
Total adult colonies	240	49	213	553	310	781	800	904	653	2036	2467	4503
Total adult density (col/m ²)	2.4	0.49	2.13	6.91	3.1	8.58	8	9.04	12.71	5.88	4.93	5.32
Broadcasting species	6	1	3	4	7	9	4	6	8	10	9	10
Brooding species	2	2	3	1	4	3	3	2	3	6	4	6
Mixed and unknown mode	4	3	3	6	6	3	0	3	7	12	8	15







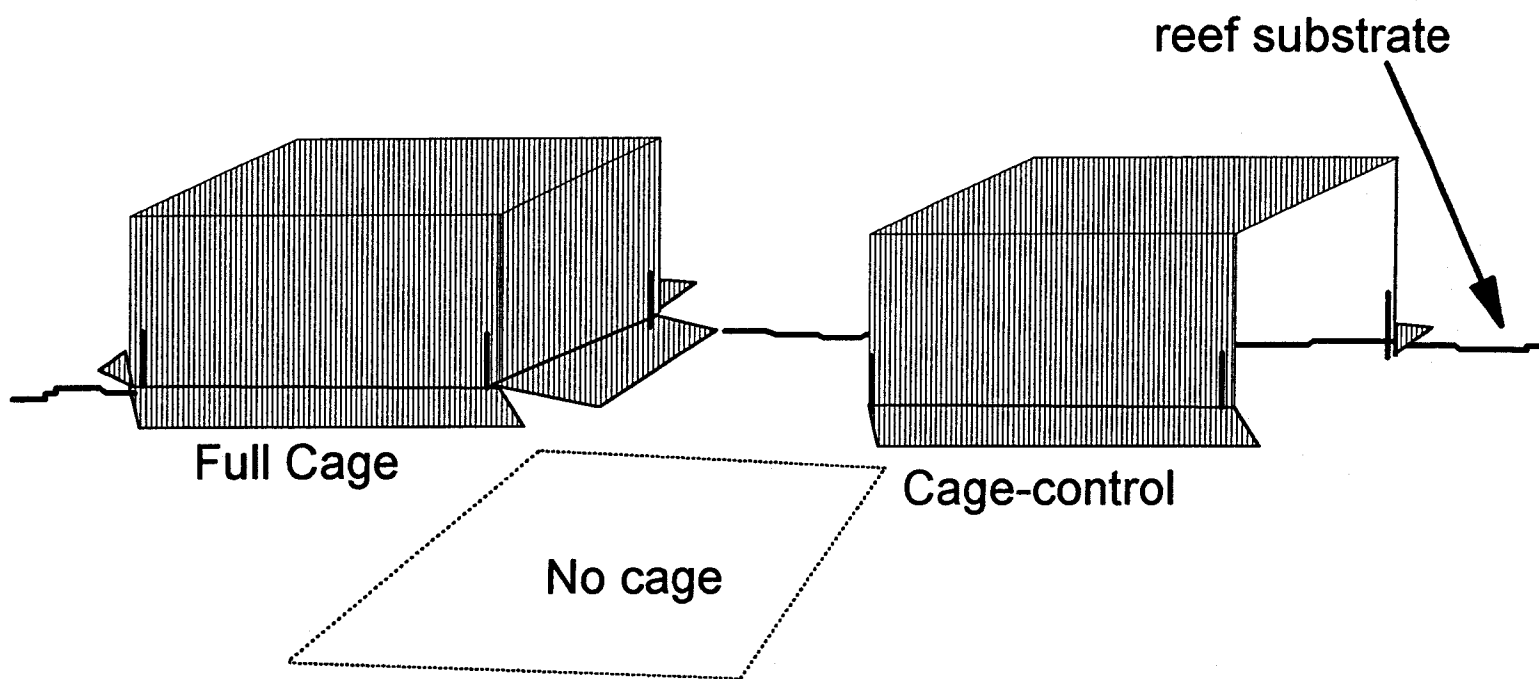
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Recruitment patterns and grazing regime as factors structuring reef benthic
communities in Biscayne National Park, USA.

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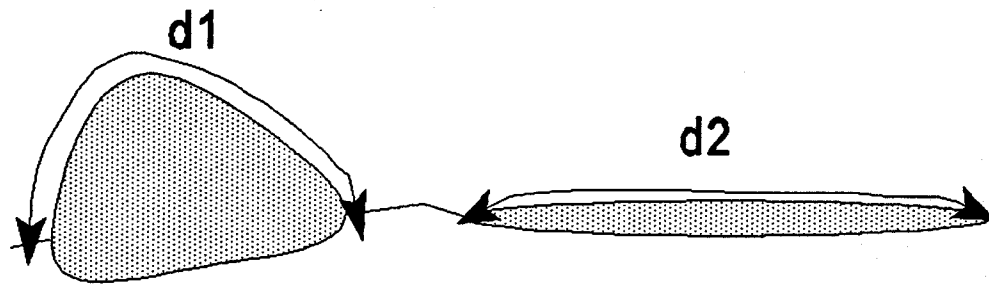
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ABSTRACT

Outer bank-barrier reefs in Biscayne National Park (BNP), Florida, USA have depauperate coral communities with little relief and few large corals while mid-shore patch reefs support greater cover and richness of corals despite more stressful temperature regimes. The role of recruitment limitation as a cause of low hard coral abundance in the bank-barrier reef communities was assessed by examining 1) size-frequency distributions of coral populations, 2) recruitment to permanent quadrats (.25 m²) on natural reef substrate, and 3) juvenile and adult coral densities. These data show that while recruitment is comparable between reef types, large coral colonies are virtually absent from the bank-barrier reefs. This suggests that juvenile survival, not recruitment rate, is limiting corals offshore. A caging experiment showed that grazers (especially parrotfishes) imposed higher levels of mortality on coral juveniles at a bank-barrier site than at an adjacent patch reef. Grazer exclusion also resulted in a significantly higher degree of macroalgal proliferation at the bank-barrier reef. Thus, recruitment limitation does not appear to explain the impoverished coral communities on offshore bank reefs in BNP. Instead, high levels of juvenile coral mortality, including high grazing loss, appear to be the dominant factor structuring these communities.

KEY WORDS: coral, corallivory, Florida, grazing, recruitment,

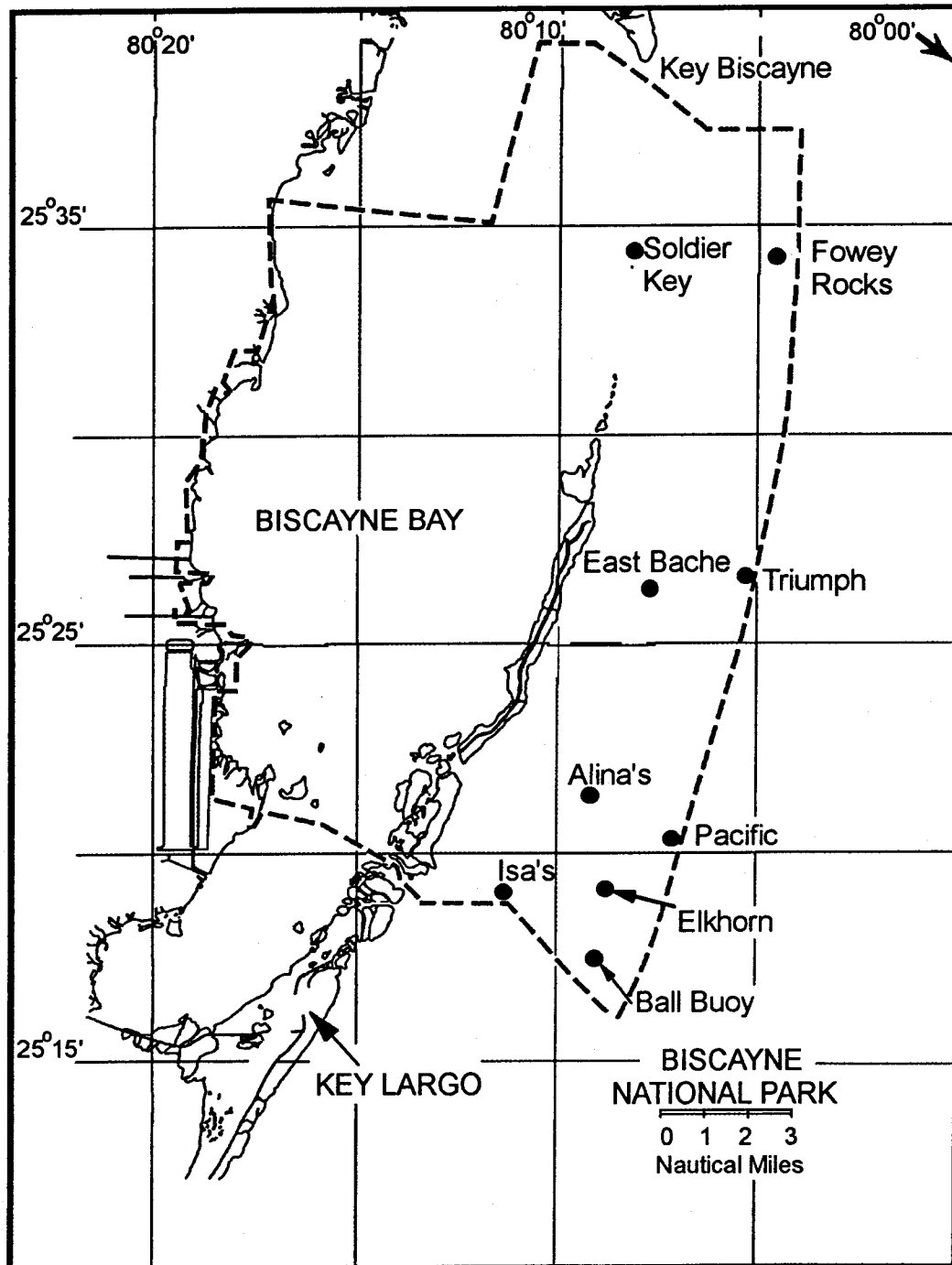
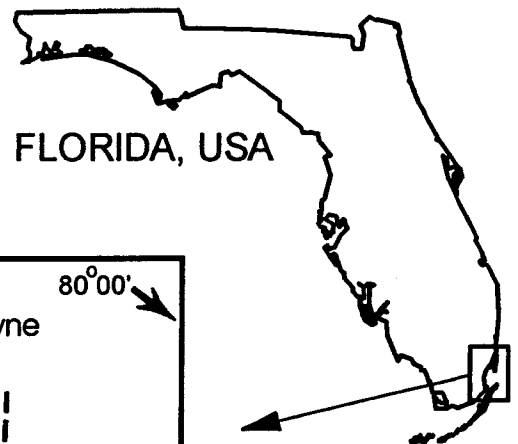


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INTRODUCTION

Biscayne National Park (BNP) lies at the northern fringe of the Florida reef tract, and indeed at the latitudinal fringe of global coral reef distribution. Many seemingly suitable offshore hardbottom sites within the Park have very little relief and low coral cover, while the mid-shore patch reefs contain greater cover and richness of corals. Paradoxically, the physical environments of the mid-shore areas, with greater terrestrial and bay influence, would appear to be more, not less stressful for corals in terms of temperature and turbidity (Weil et al. manuscr. in prep., Table 1). Thus, it is not clear how to explain this spatial variation in benthic community structure. One possible cause is lower rates of coral recruitment to the offshore sites.

Studies of coral recruitment in the Caribbean have found variable rates of recruitment characterized by dominance by small species which brood their larvae, especially *Agaricia agaricites* and *Porites astreoides* (Bak & Engle 1979, Rogers et al. 1984, Smith 1992, Chiappone & Sullivan 1996). They observed a general lack of recruitment by large frame-building species which tend to be broadcast spawners such as *Montastraea* spp., *Acropora* spp., *Diploria* spp., and *Siderastrea siderea*. In the Pacific, where recruitment patterns are often dominated by short-lived spawning *Acroporas*, it has also been suggested that recruitment at high latitude sites is relatively low and dominated by brooding species (Harriot & Banks 1995). Another study reported no sexual recruitment of massive scleractinian corals at two bank reefs in Biscayne National Park from 1989 to 1991 (Porter & Meier 1992) while artificial settlement plates at these sites yielded only 0.6 to 1.9 settlers m⁻² yr⁻¹ (J. Tougas pers.



comm). Thus, it is plausible that recruitment limitation might explain the depauperateness of coral communities and the rarity of large coral colonies at these offshore sites.

Coral reef communities are characterized by intense levels of grazing (Hatcher 1981, Carpenter 1986, Hay 1991). Intermediate levels of grazing may be optimal for controlling algae and other encrusting organisms that compete with corals for space while not inflicting mortality on coral recruits by direct predation or incidental ingestion (Birkeland 1977, Brock 1979, Sammarco 1980, 1982, Birkeland & Randall 1981, Rogers 1984).

There are few quantitative studies concerning relative grazing intensity among reef habitats within the Florida Keys. Schmitt (1997) is the notable exception, but did not examine grazing intensity on patch reefs. Given the substantial evidence that variations in grazing regime have profound influence on reef benthic community structure in general (Lewis 1986, Hughes et al. 1987, Carpenter 1990), and on coral recruitment in particular (Sammarco 1980, 1982, Birkeland & Randall 1981, Rogers et al. 1984), variation in grazing pressure is another plausible explanation for the observed differences between BNP nearshore and outer reefs benthic communities.

The current study investigated these two hypothesized mechanisms (recruitment limitation and differential grazing impacts) for maintaining observed differences in coral community structure of BNP reefs. Firstly, the population size frequencies and patterns of recruitment for scleractinian corals on different reef types (depauperate offshore bank versus more-developed mid-shore patch reefs) were examined to

Figure 11. Hypothesized feedback loops between development and maintenance of physical reef structure, grazing, and juvenile coral survivorship.

determine if recruitment limitation precludes significant coral development on the bank-barrier reefs. Secondly, a two-way factorial field experiment was conducted to determine if grazing influenced benthic community structure on these reefs and whether this influence differed between sites.

METHODS

Site descriptions:

The study sites were seven reefs within Biscayne National Park (BNP)(Figure 1). Quantitative sampling of benthic communities and several environmental factors were conducted during 1994-95. These sites were chosen to include pairs of nearshore patch reefs and offshore bank reefs spanning the north/south extent of the Park. We report detailed quantitative descriptions of these sites elsewhere (Weil et al. manuscript in prep.). Summary site descriptions are given in Table 1. No significant variation in total sediment deposition rates was found between reef types, though nearshore resuspended sediments had smaller particle composition and higher nitrogen content than offshore sites (Weil et al. manuscript in prep.).

Population Size Frequency Distributions

Size frequency distributions of four common species of hermatypic corals were measured at two offshore bank-barrier reefs (Pacific and Triumph), two mid-shore patch reefs, (East Bache and Isa's reefs) and one bank reef of intermediate location (Ball Buoy). The species sampled were *Siderastrea siderea*, *Porites astreoides*,

(A) Cumulative juvenile density in the 0.25 m² permanent quadrats, numbers in bars are numbers of quadrats at each site. (B) Juvenile density in belt transect sampling (n=80-100 one-m² quadrats sampled along four or five belt transects at each site).

Figure 7. Overall mortality of juveniles in permanent quadrats for a one-year interval, and subdivided by reproductive. Mortality expressed as mean percent (+1 s.e.) of juveniles present in the initial census. Number of quadrats given in each set of bars.

Figure 8. Abundance of juvenile corals sampled in the belt transect sampling. (A) Density of juvenile colonies (#/m²). (B) Juveniles as a percent of total 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 $p > 0.05$).

Figure 9. Results of the cage transplant experiment. (A) Percent mortality (+ 1 s.d.) of coral transplants one week after transplantation into three caging treatments at one mid-shore patch reef (East Bache) and one offshore bank reef (Triumph). P-values from a two-way ANOVA. (B) Percent cover of macroalgae (mean + 1 s.d.) within the cage treatment areas, measured at the end of the 10-week experiment. P-values from a two-way ANOVA.

Figure 10. Results of 3-hr plant grazing assay at East Bache and Triumph reefs. Proportion of pieces of each plant species consumed at each site. P-values shown are from Fisher's Exact tests.

Montastraea cavernosa, and *Montastraea faveolata*. Haphazard colonies of each species within 6 m wide belt transects (four or five transects at each site, 20-25 m apart) were measured, striving to obtain a minimum sample size (>100) for each species. Care was taken not to overlook small colonies. At sites where a species was rare, sample sizes were significantly smaller than the desired 100 (noted on graphs). No data are presented for those sites where *M. faveolata* was so rare that a reasonable sample could not be obtained. Sizes presented are based on an 'over-the-top' measurement made with a measuring tape along the longest diameter since it provides a good integration of both vertical and lateral growth (Figure 2).

Permanent Quadrats:

Permanent (0.25 m²) quadrats were established (designated with nails driven into the reef substrate) at three sites to monitor recruitment and survival of small scleractinian colonies. The quadrats were selectively placed on relatively flat, "bare" substrate, i.e. areas without macro-organisms, to maximize the potential recruitment observed. The sites were East Bache (mid-shore patch reef), Triumph (offshore bank-barrier reef), and Ball Buoy (southern, well-developed bank reef). Ten quadrats were established at Triumph and Ball Buoy, 15 quadrats at East Bache. These quadrats were fanned clean of sediment and examined closely with a magnifying glass (10x) to identify new recruits and juveniles (less than 2 cm diameter). The quadrats were mapped, and occurrence of juveniles was enumerated at an initial census during fall of 1994 and recensused one year later in November 1995. The survival or loss of

FIGURE LEGENDS

Figure 1. Map of Biscayne National Park showing approximate location of study sites.

Figure 2. Illustration of "over the top" dimension used for constructing population size frequency distributions.

Figure 3. Schematic design of three treatments used in the caging experiment. Ten to 15 juvenile corals were transplanted into each cage/plot at each site. Five such replicates were maintained at each site.

Figure 4. Size frequency distributions for four species at five sites. Size categories: 1=0-9.5cm, 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.

Figure 5. Mean (+1 s.e.) density of new recruits during two censuses of the permanent quadrats at three reefs in Biscayne National Park. P-values from Kruskal-Wallis one way nonparametric ANOVA. For the second census, bars with the same letter do not differ significantly (Dunn's post-hoc test, $p > 0.05$).

Figure 6. Average densities (+1s.e.) of juvenile corals of species with brooding versus broadcasting reproductive mode at each site as determined by two sampling methods.

juveniles from the first census and recruitment of new juveniles in each quadrat was noted.

Belt Transect Sampling of Juvenile Colonies:

Twenty 1 m² quadrats were sampled at 3-5 m intervals along five belt transects (four on the smaller patch reefs) 20-25 m apart for a total of 80 to 100 m² sampled at each site listed in Table 1. Abundance and cover of juvenile coral colonies were noted. Juveniles were defined to be less than 5 cm diameter for large species such as the *Montastraea* spp., *Diploria* spp., and *Siderastrea siderea* or less than 2 cm diameter for small-sized species (e.g. *Porites astreoides*, *Favia fragum*). 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 latter two groups are not reported here.

Caging Experiment:

Differential effects of grazing on benthic communities between reef sites was assessed with a caging experiment at one patch (East Bache) and one bank-barrier (Triumph) reef. Five cages (0.5x0.5x0.3 m) and five half-cage controls (2 walls and roof) were attached to eyebolts epoxied into the reef substrate at each site (Figure 3). A mixed species assemblage of juvenile corals was epoxied onto the natural reef substrate in each cage and to adjacent uncaged plots (no-cage controls). Around 10-15 colonies of 4 or 5 species including *Porites astreoides*, *P. divaricata*, *Favia fragum*,

Table 3. Visual census data for herbivorous fishes (total Scarids and Acanthurids) at sites in Biscayne National Park. Data are mean number of fish observed in individual stationary visual census samples each year at nearshore patch reefs, offshore bank reefs, and Ball Buoy. Source:Bohsack and McClellan, US.National Marine Fisheries Service, unpublished data.

PATCH REEFS				BANK/BARRIER REEFS				
SITE	Star coral	Alinas	IGW Trust	Ajax	NE Corner	Brewsters	Triumph	Ball Buoy
1988	18.8	40.3	38.1	25.3	14.4	24.4		27.6
1989		21.9	32.8	23.1	22.3	24.3	20.3	29
1990	31	21.5	33.9	18.7	19.1	33.7	18.5	13.3
1991			17.9	14.3	12	14.8	15.8	9.6
1992				17.9	17.5	19.8	32.1	
1995	27.5	24.9	12.1	14.3	13.3	19.3	16	12.8
MEAN/site	25.8	27.2	27.0	18.9	16.4	22.7	20.5	18.5
MEAN/reef type		26.7				19.4		

Siderastrea radians, and *Isophyllia sinuosa* were placed in each cage or plot. Coral survival was censused after one week and at the end of the 10-week experiment. Proliferation of algae was assessed using a grid to estimate percent cover of macroalgae at the end of the experiment. Each response variable was analyzed in a separate two-way analysis of variance to determine the effects of cage treatment and site.

Plant Grazing Assays:

A direct assay of plant consumption was conducted at the same sites as the caging experiment (East Bache and Triumph). Four plant sprigs (the seagrass *Thalassia testudinum*, the green seaweed *Caulerpa racemosa*, and two brown seaweeds, *Lobophora variegata* and *Dictyota* sp.) were attached to 30 cm lengths of three-stranded rope. The ropes were attached by one end to the reef substrate at each site (n=14 or 15 ropes) for a period of 3 hours. As the ropes were collected, each plant was scored as uneaten, half eaten, or completely consumed. Data were subjected to contingency analysis (Chi-squared or Fisher's Exact test) to compare the proportion of plant pieces eaten and uneaten between sites.

RESULTS

Population Size Frequency Distributions

The outer bank-barrier reefs, Pacific and Triumph, had a qualitatively distinct pattern of coral colony size frequencies with populations being severely skewed (in

Table 2. Turnover of recruits in the permanent quadrats by species. "Surviving" indicates mean density (# recruits/m²) of colonies less than 2 cm diameter identified at the initial census in fall 1994 and relocated alive one year later. "Dead" indicates mean density of recruits identified in the first census that were missing in the final census. "New" indicates mean density of recruits appearing during the one year interval.

	East Bache				Triumph				Ball Buoy		
	surviving	dead	new		surviving	dead	new		surviving	dead	new
<i>Siderastrea siderea</i>	2.13	1.07	8.80		1.60	0.80	0.00		0.40	0.40	1.20
<i>Porites astreoides</i>	2.67	1.07	3.20		2.40	0.40	0.40		3.60	1.60	0.40
<i>Agaricia agaricites</i>	0.00	0.27	1.60		2.40	1.20	0.80		2.40	0.80	0.00
<i>Favia fragum</i>	0.53	0.53	0.27		0.80	0.00	0.00		2.80	0.80	0.80
<i>Porites porites</i>	0.00	0.00	0.00		0.00	0.40	0.40		0.80	0.00	0.80
<i>Dichocoenia stockesii</i>	0.00	0.27	0.00		0.00	0.00	0.00		0.00	0.00	0.00
<i>Mycetophyllia</i> spp.	0.27	0.00	0.53		0.00	0.00	0.00		0.00	0.00	0.00
<i>Montastrea faveolata</i>	0.27	0.00	0.00		0.00	0.00	0.00		0.40	0.00	0.00
<i>Leptoseris cucullata</i>	0.00	0.00	0.00		0.00	0.00	0.00		0.40	0.00	0.00
<i>Eusmilia fastigiata</i>	0.00	0.00	0.80		0.00	0.00	0.00		0.00	0.00	0.00
<i>Millepora</i> spp.	1.00	0.00	0.00		0.00	0.00	0.00		0.00	0.00	1.20
Total(#/m ²)	6.86	3.20	15.20		7.20	2.80	1.60		10.80	3.60	4.40

some cases, truncated) toward small size classes (45-90% of populations in the smallest <10 cm size class). At these two sites, larger size classes are virtually absent (Figure 4). Overall coral abundance is also depressed at these sites, reflected in the small sample sizes for *Montastraea cavernosa*, *Porites astreoides*, and *Montastraea faveolata* (Figure 4) for which insufficient colony numbers were encountered to display the data. In contrast, the patch reefs, East Bache and Isa's, along with the mid-shore bank reef Ball Buoy had much more even size distributions with both small and large size classes well represented. These sites are also the only ones where sufficient numbers of *M. faveolata* were encountered to estimate size frequency distribution.

Recruitment Quadrats:

In the initial census of the recruitment quadrats (Figure 5), the density of recruits did not differ significantly among the three sites (Kruskal-Wallis ANOVA $p=0.46$). However, the number of colonies recruiting into the quadrats at these sites during the subsequent one-year interval showed quite a different pattern with significant variation among sites (Kruskal-Wallis $p=0.019$). 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 (Figure 5). Even when one outlying quadrat at East Bache (in which 26 new recruits appeared during the one year interval) is excluded, the density at East Bache was still $7.1/m^2$ and the Kruskal-Wallis non-parametric ANOVA still indicated significant variation in recruitment among the sites; however, none of the pairwise comparisons were significant. Thus, the patch reef, East Bache, had high

TABLE 1: Environmental and biotic characteristics for sites examined in this study.

Patch reefs are in midshore areas while bank reefs are along the offshore shelf edge.

Extreme temp. indicates percent of days monitored when average temperature was

above 30°C or below 20°C. Sediment deposition (mean of 13 two-week trap

deployments) in mg/cm²/day. Data are from Weil et al. (in prep.) except where noted.

SITES	East Bache	Triumph	Alinas	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 (m)	1-5	3-7	2-6	2-10	1-5	2-8	2-6
Reef type	patch	bank-barrier	patch	bank-barrier	patch	midshelf 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	3.1	3.4	3.5	4.5	8.8	14.2	1.8
Estimated underwater visibility (ft) ¹	n.a.	37	18	n.a.	n.a.	36	n.a.

1. Bohnsack et al. 1992

numbers of recruits during both census periods while the adjacent bank-barrier reef had comparably high numbers of recruits during the first census, but significantly lower levels during the second.

The massive broadcast spawner, *Siderastrea siderea*, was the most common species of recruit at East Bache contributing almost half of all recruits (Figure 6A). Brooders such as *Porites astreoides*, *Agaricia agaricites*, and *Favia fragum* were most abundant at Triumph and Ball Buoy (Figure 6A). There was a slight trend for higher overall juvenile mortality at Ball Buoy (Figure 7), though mortality rates did not differ significantly between sites (Kruskall-Wallis $p=0.2908$) nor between corals of differing reproductive modes (Figure 7).

Belt transect sampling of juvenile colonies

Densities of juveniles estimated from the belt transect sampling were much lower than those measured in the permanent quadrat sampling (Figure 6) due to differing intensity of search in the two methods. However, though there was significant variation in juvenile density among sites, (Kruskall-Wallis $p<0.001$) there were similar densities of juvenile scleractinians for each patch/bank reef pair at similar latitude (Dunn's test $p>0.05$ for East Bache versus Triumph and for Alina's versus Pacific, Figure 8). The proportions of total coral colonies that were juveniles was significantly higher at Triumph and Pacific than at their adjacent patch reefs, East Bache and Alina's, due to lower adult density ($p<0.05$ by post-hoc Dunn's tests, Figure 8B). The southern patch reefs, Elkhorn and Isa's, had significantly higher densities of juveniles

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than the other reefs ($p < 0.05$ by post-hoc Dunn's tests, Figure 8A). These reefs had a high proportion of juveniles because of the high juvenile density at these sites (Figure 8A).

Juveniles of the massive broadcaster *Siderastrea siderea* were the most abundant on the bank-barrier reefs (Triumph and Pacific), as well as the northern patch reef East Bache. *Porites astreoides* was the species with higher abundance of recruits on the more southern Elkhorn, Alina's and Ball Buoy reefs.

Caging Experiment:

The caging experiment showed that transplanted juvenile corals experienced dramatic attrition from grazing in a very short time span. We directly observed parrotfishes, especially *Sparisoma aurofrenatum*, eating the transplants. At the one week census, almost 100% of the transplants in full cages at both sites were intact, while 30-75% of the transplants in half-cage and no-cage controls were missing or dead (Figure 9A). Two-way ANOVA (SITE * CAGE treatment) on percent of transplants missing or dead from each cage (arcsin transformed, $n=5$) showed no statistical interaction of site and cage treatment ($p=.117$). Full cages had significantly higher survival of transplants (CAGE $p < 0.0001$) than either half-cage or no-cage controls which did not differ from each other, (SNK $p > 0.05$). Also, survival was significantly greater at the patch reef, East Bache, than at the bank-barrier reef, Triumph (SITE $p=0.003$).

Macroalgae proliferated in the full cages during the 10 weeks that large grazers

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were excluded (Figure 9B). Two way ANOVA on percent cover of macroalgae in each cage or plot at ten weeks indicated a significant interaction of site and cage treatment, resulting from greater proliferation of macroalgal cover in full cages at Triumph than at East Bache, and a similar lack of proliferation in half and uncaged treatments at both sites. That is, grazers had a significantly stronger effect on preventing algal overgrowth at Triumph than at East Bache.

Plant Grazing Assay:

Results of the plant grazing assay did not reveal any differences in grazing intensity between the two sites when all plants were considered together (Figure 10, Chi-squared contingency test, $p=0.213$, $n=14$ and 15). In a species by species analysis, Fisher's Exact tests showed that *Caulerpa racemosa* was the only plant tested for which there was a significant difference between sites ($p=0.05$) with greater grazing intensity at the patch reef, East Bache (Figure 10). *Dictyota* spp. and *Lobophora variegata* also showed a trend toward greater consumption at the patch reef while the trend for *Thalassia testudinum* was for greater consumption at the bank-barrier reef (Figure 10).

DISCUSSION

Corals at the early stages of recruitment are very small and difficult to see, especially in high relief areas with high cover of encrusting organisms, and so obtaining accurate estimates of *in situ* coral recruitment rates is difficult. Coral recruitment

estimates generated by studies using large (1 m^2) quadrats appear to greatly underestimate the abundance of juvenile corals. Our values for juvenile coral density generated from belt transect sampling at 1 m^2 scale (Figure 6B) are comparable to those reported by Chiappone & Sullivan (1996) in the range of 1.2-3.4 juveniles m^{-2} . However, juvenile density estimates from 0.25 m^2 quadrats that we placed preferentially on flat, clear substrate and examined with a more intensive search strategy were an order of magnitude higher (Figure 6A). Therefore, contrary to other reports (Porter & Meier 1992, Tougas pers. comm.) that state that few or no corals are recruiting to BNP reefs, we find relatively high numbers of small corals on many of these reefs (Figure 8A) including large numbers of the broadcast-spawning, framework-building *Siderastrea siderea*.

A comparison of juvenile densities between paired patch reef and barrier reef sites (i.e. within the same region of the Park) suggests that recruitment rates are similar for the two reef types (Figure 8A). Survival rates of these juveniles at the offshore sites, however, must be lower to produce the skewed size-frequency distributions (Figure 4) estimated from wide scale sampling of these habitats. Some combination of factors, potentially greater abrasion or grazing mortality, appears to decrease the survivorship of the offshore recruits with the long term consequence being a scarcity of larger coral colonies on the offshore reefs. Our mortality estimates based on the permanent quadrats are similar to the $33\% \text{ yr}^{-1}$ reported by Bak & Engle (1979) for Curaçao, and Smith (1992) for Bermuda but do not differ between sites (Figure 7). However, these estimates reflect a small sample size of relatively flat substrate over a

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limited time interval (only one year) whereas the belt transect samples incorporate the spatial heterogeneity of each habitat and integrate a much longer time scale.

The most salient feature of the spatial pattern in juvenile density is the significantly greater densities on reefs in the southern region of the Park (Figure 8A). The southern region of Biscayne National Park borders on John Pennekamp Coral Reef State Park and the Key Largo National Marine Sanctuary, and these southern BNP reefs are more typical of the true Florida Reef Tract. Historical "inimical" waters may be the primary determinant of this north/south spatial gradient (Shinn et al. 1989). Burns (1985) suggested that both cold water and sediments associated with outflux of bay waters from the north was limiting to shallow reef corals in Biscayne National Park, especially at Triumph Reef.

The patch reefs, with their large massive colonies, have much greater physical structure and spatial heterogeneity than the flat, relict platforms of the offshore reefs. It might be expected that the greater patch reef physical structure provides shelter and protection with a consequent higher survival of juvenile corals at these patch reef sites. This is in fact the trend deducible from the size frequency distributions (Figure 4) as well as the caging experiment.

Visual census data of grazing fishes (all scarid and acanthurid species combined) over a period of six years at multiple patch reefs and bank-barrier reefs in Biscayne National Park indicate that areal densities of these fishes are actually lower on bank reefs than the patch reefs (Table 3, NMFS unpublished data, Bohnsack & McClellan, pers. comm.). These reef fish populations are no doubt also responding to

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increased shelter availability at the patch reef sites (Grigg 1994). The greater grazer abundance is in agreement with the trend for higher grazing loss at the patch reef site of experimental plants which were presented conspicuously above the substrate (Figure 10). However, greater grazing mortality on juvenile corals was observed at the bank reef site (Figures 9A). Juvenile corals are small and flush with the substrate and may be more difficult for the fishes to detect on the more complex patch reef substrates. Therefore, even though there are more grazing fishes on the patch reefs, they may cause less mortality to coral recruits in complex environments. Figure 11 illustrates these hypothesized feedback loops between substrate complexity, coral survivorship and grazing pressure. Greater exposure may subject small corals on the bank reefs to increased stress or mortality from other physical disturbances as well. Such mechanisms fostering or precluding the development of physical structure may have broad implications for reef trophodynamics, nutrient cycling, and ecosystem function (Szmant in press).

In this study, the caging experiment provided some explanation for variations in benthic community structure between bank and patch reefs. Juvenile corals at the offshore bank reef suffered higher mortality from grazers (Figure 9A) and this pattern is consistent with aspects of community structure such as low coral density, low percent coral cover, and the smaller size of corals at the offshore reefs. However, absolute levels of grazing mortality in the experiment may have been elevated over levels experienced by naturally occurring recruits due to the novelty of epoxy and concentrated diver activity.

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There are conflicting results regarding the amount of damage inflicted on Caribbean reef corals by herbivorous fishes (Hixon 1997). Observations by Glynn (1973) and Frydl (1979) and other experimental results (Miller & Hay in prep.) indicate that direct predation of corals by fishes, especially parrotfishes, can be significant. Randall (1974) and Bak & Engle (1979) report grazing fishes to damage juvenile corals. In contrast, Birkeland (1977) suggested that grazing fishes in Panama actively avoided consuming even very small (3mm) coral recruits, and Fitz et al. (1983) showed higher survival and/or growth of recruits exposed to grazers compared to those protected by cages. In any case, it seems unlikely that differential grazing intensity is the sole reason for the dramatic lack of corals at the offshore sites in Biscayne National Park (Triumph Reef, Pacific Reef, and others). Physical factors such as abrasion during high-energy events and sedimentation regimes are no doubt also at play.

In conclusion, we found no evidence to support the hypothesis that coral settlement and recruitment processes consistently vary between depauperate offshore bank reefs and nearshore patch reefs. In fact, coral recruitment rates at all sites were substantially higher than has been previously reported. The current study supports the hypothesis that variation in grazing intensity, perhaps interacting with variation in structural complexity between patch and bank reefs, plays a strong role in controlling variation in coral abundance on Biscayne National Park reefs. Our results suggest the possible operation of a feed-back loop which depends on the presence of large coral colonies to provide physical structure on nearshore patch reefs, which, in turn, promotes coral recruit survival and maintenance of structure (Figure 11). Physical

factors that can limit juvenile coral survival on offshore reefs may also limit the amount of coral accumulation which in turn leads to greater juvenile coral loss due to other processes such as fish grazing.

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