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REPORT

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High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA

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Abstract Baseline studies conducted in 1998 document the presence of robust, non-reef-building *Acropora cervicornis* thickets in shallow (3–7 m depth), near-shore waters off the coast of Fort Lauderdale, Florida, USA. These thickets thrive in a high-latitude environment, the northernmost in the continental USA, in the midst of potential anthropogenic stressors. Within thickets, the spatial variation in mean percent coral cover, macroalgal cover, scleractinian species richness, density of *A. cervicornis* juveniles, and the density and size of *A. cervicornis* colonies and fragments were recorded. Thicket size ranged between ~0.1 and 0.8 ha and mean coral cover varied between ~5 and 28%, with *A. cervicornis* accounting for ~87–97% of all scleractinians. Mean *A. cervicornis* colony and fragment densities per thicket were 1.3–3.3 colonies m^{-2} and 0.7–2.8 fragments m^{-2}, respectively. Recruit densities varied between 0 and 1 ind. m^{-2}. White band disease was detected at all thickets, with a mean *A. cervicornis* colony surface area affected of 1.8%. For all thickets, densities of the coral-livorous polychaete *Hermodice carunculata* ranged between ~18 and 86 ind. ha^{-1}, with predation scars affecting < 0.2% of the *A. cervicornis* cover. These flourishing *A. cervicornis* thickets off Fort Lauderdale provide an interesting counterpoint to the declining and disease-stricken *A. cervicornis* populations reported in the Florida Keys and wider Caribbean.

Keywords *Acropora cervicornis* · Fort Lauderdale · Distribution · Abundance

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Introduction

Since the late 1970s, *Acropora cervicornis* (staghorn coral) populations have experienced extreme and widespread decline in many areas throughout the Caribbean (Aronson and Precht 2001a). Reductions of up to 98% in live coral cover have been recorded in some areas (see Miller et al. 2002), with no apparent analogue in the recent (~3,800 years before present) geological record (Aronson and Precht 1997, but see Miller et al. 2002). Thus, the US National Marine Fisheries Service has listed *A. cervicornis* as a candidate species as per the Endangered Species Act (Federal Register vol. 64, no. 120, 23 June 1999, pp 33466–33467; Diaz-Soltero 1999).

Major causes of staghorn coral mortality include storm damage, thermal stress, nutrient loading, white band disease (WBD), sedimentation, and invertebrate predation (see review by Aronson and Precht 2001b). From the late Pleistocene and into the Recent (~500,000 years; Jackson 1994), *A. cervicornis* played a major structural and ecological role in many Caribbean reefs, contributing significantly to reef accretion, framework construction, and habitat formation (Aronson and Precht 2001a). *Acropora cervicornis* losses have been associated with phase shifts in coral community structure, increased abundance of macroalgae, as well as reduced rates of coral reef accretion (Precht and Aronson 1997; Aronson and Precht 2001a). For example, since the 1980 WBD-related *A. cervicornis* population collapse in Belize, macroalgal abundance has increased by 300 and 1,200% at Glovers Reef Atoll and Carrie Bow Cay, respectively, over the past two decades (McClannahan et al. 1999). Additionally, it has been proposed that the predominance of asexual reproduction combined with limited long-distance larval dispersal capabilities have led to small effective population sizes and low genotypic diversity in *A. cervicornis*, resulting in increased susceptibility to disease (see Bak 1983). Thus, the potential for natural recovery of *A. cervicornis* populations Caribbean-wide remains uncertain (Precht et al. 2002).

During previous research undertaken by the National Coral Reef Institute (NCRI) and Nova Southeastern University Oceanographic Center (NSU-OC) personnel, robust *A. cervicornis* thickets were discovered in shallow (3–7 m depth) coastal waters off Fort Lauderdale, Florida. These thickets thrive in a high-latitude environment, the northernmost in the continental USA, and in areas apparently subject to significant natural and anthropogenic impacts, including thermal stress, pollution, increased fresh water discharge, periodic ship groundings, and extensive coastal urbanization (Thomas et al. 2000). This paper reports on the distribution, abundance, and ecological structure of the *A. cervicornis* thickets off the coast of Fort Lauderdale. Data on the incidence of WBD and fire worm (*Hermodice carunculata*) predation are also presented.

Materials and methods

Study area

The near-shore marine environment off the coast of Fort Lauderdale, Florida, is characterized by a Pleistocene coquina limestone or beachrock platform, known as the Anastasia Formation (Cooke 1945). A series of sub-parallel ridges, small ledges, solution holes, and pockets of sediments characterize this feature, which has been interpreted as shoreline deposits submerged during the late Pleistocene to early Holocene (circa 4,000–19,000 years before present; Raymond 1972). This shallow benthic environment supports rich faunal assemblages dominated by octocorals, algae, sponges, and stony corals, similar to those described by Goldberg (1973) for adjacent Palm Beach County, Florida. Currently, there is no active reef accretion in these shallow coastal waters (see Jaap 1984).

Water circulation and oceanographic conditions off the coast of Fort Lauderdale are primarily determined by the flow of the Florida Current. Mean current speed ranges between 7 cm s^{-1} in March and April and 20 cm s^{-1} in July, with differences probably controlled by seasonal increases in volume transport (Niler and Richardson 1973). Current reversals are related to cyclonic eddies, which produce a strong southward coastal flow, and are accompanied by marked turbidity fluctuations and high salinity perturbations (≥36.4‰) (Lee 1975; Lee and Mayer 1977). Surface water temperatures range from 22–25 °C in the winter and from 28 to ~30 °C during the summer (http://ferret.wrc.noaa.gov/las1/climate_server). However, thermal excursions of < 20 and > 30 °C can occur during atypical years.

Methodology

All sampling took place between April 2001 and August 2002. Preliminary work by Thomas et al. (2000) and anecdotal accounts by NSU-OC students and personnel were used as a baseline in locating staghorn coral thickets. Supplementary exploration and manta tow surveys were conducted to further assess staghorn coral presence and abundance in the region. Twelve discrete thickets were identified between Port Everglades (26°05.34′N; 80°06.26′W) and Hillsboro Inlet (26°15.28′N; 80°04.51′W), at approximately 3–7 m depth, ranging from 45–75 m in diameter. Seven of these (i.e., the largest and most dense) were studied in detail, and each assigned a name (Fig. 1).

At each thicket, quantitative surveys were conducted along four 50-m line transects, to document the composition and structure of the coral assemblage. Transect starting points were haphazardly selected along the northern perimeter of north–south oriented thickets, or (less commonly) along the eastern perimeter of east–west oriented thickets. Transects were defined by extending 50-m tapes, co-parallel in a north–south or east–west direction across a given thicket. On each transect, 10–15, 1-m^2 quadrats were surveyed. Quadrat position along transects was determined by random selection of single digits, with the first random digit indicating the position (in meters) of the first quadrat. Subsequent quadrat positions were determined by addition of random digits to the sum of the previously selected digits. The total number of quadrats per transect varied accordingly (see Table 1). Within each quadrat, scleractinian species richness was recorded, as well as visual estimates of percent cover of live and dead corals, density of *A. cervicornis* juveniles (< 5 cm diameter), macroalgae, coral rubble, sand, and hard bottom with turf algae. *Acropora cervicornis* colonies and fragments were also counted and measured (average canopy diameter and height, and maximum fragment length and height). For the purpose of this study, colonies were defined as those attached to the substrate, and fragments as those unattached to the substrate.

Predation by the fireworm, *Hermodice carunculata*, and the incidence of white band disease (WBD, see Antonius 1981; Santavy and Peters 1996; Precht and Aronson 1997) were also documented along two additional 50-m, haphazardly selected transects within each thicket. Between 10 and 20, 1-m^2, randomly selected quadrats per transect were surveyed at each thicket. Transect and quadrat placement methodology followed that used for community structure surveys. Only quadrats containing live *A. cervicornis* were surveyed. Within each quadrat, live *A. cervicornis* cover and percent cover of WBD were recorded, as well as number and size of scars caused by fire worm predation. Only branch tip scars clearly attributable to *H. carunculata* predation were recorded (see Knowlton et al. 1990). Corallivory and WBD surveys were conducted during the warmest period of 2002 (i.e., June–August), since the incidence of WBD has been observed to increase as a function of water temperature (see Santavy and Peters 1996).

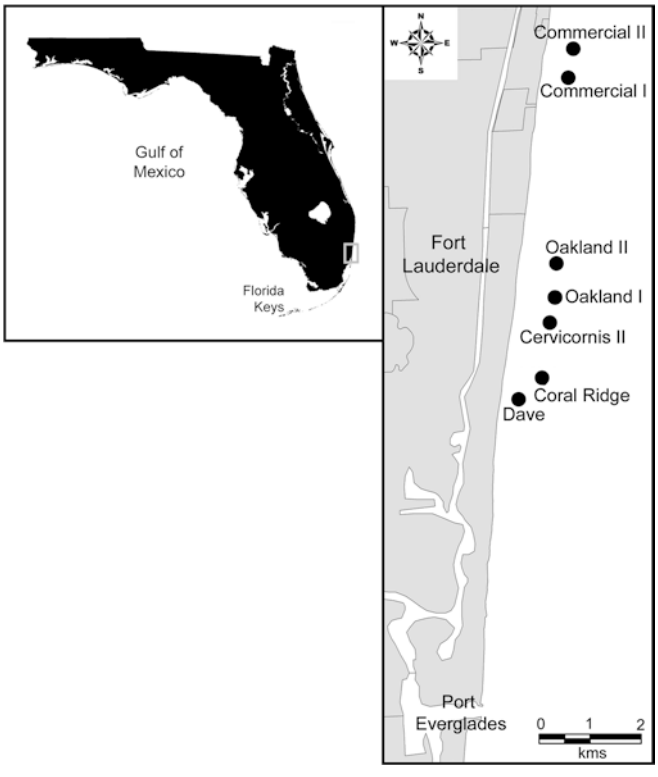

Fig. 1 Location of *Acropora cervicornis* study thickets off coast of Fort Lauderdale, Florida

Table 1 Depth, approximate distance from shore, estimated area, total number of quadrats surveyed, and scleractinian species richness at the study thickets (species listed alphabetically). *A Acropora cervicornis*; *B Agaricia agaricites*; *C Agaricia humilis*; *D Colpophyllia natans*; *E Dichocoenia stokesi*; *F Diploria clivosa*; *G Diploria strigosa*; *H Madracis mirabilis*; *I Meandrites meandrites*; *J Montastraea annularis*; *K Montastraea cavernosa*; *L Montastraea faveolata*; *M Porites astreoides*; *N Porites porites*; *O Siderastrea radians*; *P Siderastrea siderea*; *Q Stephanocoenia michelinii*

Item	Dave	Coral Ridge	Cervicornis II	Oakland I	Oakland II	Commercial I	Commercial II
Mean depth (m)	6	6	4	4	4	6	6
~Dist. from shore (m)	380	840	770	790	740	600	560
~Area (m^2)	3,300	7,900	1,700	1,900	1,900	1,400	1,000
No. quadrats surveyed	48	52	48	46	50	48	50
Scleractinian spp. richness	A,C,G,H,L, M,N,O (8)	A,B,C,E,H,L, M,O,P,Q (10)	A,E,G,M,O (5)	A,E,F,J,L, M,O,Q (8)	A,D,E,F, G,M,O (7)	A,E,G,I,L, M,N,O (8)	A,E,F,G,K, L,M,O (8)

Non-parametric Kruskal-Wallis analyses of variance on ranks were used to compare benthic cover parameters among thickets. Although mathematical transformations were applied to the original cover data, (arc-sin) transformed data did not satisfy parametric statistical requirements. Additionally, to analyze the ecological similarities among thickets, an agglomerative cluster analysis (PRIMER v5.2.4, Plymouth Marine Laboratory) was performed using percent cover of nine different benthic parameters (Table 2) (Bray-Curtis similarity measure on fourth-root transformed data; Bray and Curtis 1957). A SIMPER (SIMilarities PERcentages) analysis (Clarke 1993) was then performed to identify those benthic parameters contributing most to the clustering of groups defined by the agglomerative cluster analysis. Statistical correlations (Pearson Product Moment Correlation) were conducted to investigate the degree of association between coral cover and colony size, and between coral cover and colony densities. Statistical correlations (Pearson Product Moment Correlation) were also utilized to investigate the degree of association between percent coral cover and the incidence of disease, as well as between percent coral cover and fireworm predation. The statistical association between the incidence of disease and fireworm predation was also investigated.

Results

Acropora cervicornis thicket size ranged between ~0.1 and 0.8 ha. All thickets occurred between ~400 and 800 m offshore, at depths of approximately 3–7 m, with no signs of reef accretion. Mean coral cover ranged between ~5 and 28%, with *A. cervicornis* representing 87–97% of all scleractinians. Scleractinian species richness did not exceed ten at any given thicket. Prominent non-acroporid scleractinians observed included *Siderastrea radians*, *Montastrea cavernosa*, *Porites astreoides*, *Dichocoenia stokesi*, *Diploria* spp., and *Meandrina meandrites*. Ecological structure survey results are summarized in Tables 1, 2, and 3.

Kruskal-Wallis analyses of variance indicated that percent cover of the benthic parameters studied varied significantly among thickets ($p < 0.05$, Table 2). Live coral cover was highest at Dave and lowest at Cervicornis II. Percent hard bottom was highest at Oakland II and lowest at Coral Ridge. Density of recruits (< 5 cm diameter) ranged between 0 and 1 m^{-2}, with a mean of 0.1 recruits m^{-2} for all thickets.

Statistically significant differences were also found for mean colony size and densities among thickets (Table 3). Larger *A. cervicornis* colonies (> 100 cm diameter) occurred at thickets exhibiting both high and intermediate levels of coral cover. However, there was no statistical association between mean colony size and mean percent *A. cervicornis* cover at any thicket (Pearson Product Moment Correlation, $p > 0.05$). Mean colony densities were positively correlated with percent cover of *A. cervicornis* at all thickets (Pearson Product Moment Correlation, $p < 0.05$, Table 3). Mean fragment densities also varied significantly among thickets, whereas mean *A. cervicornis* fragment size did not (Table 3). On average, colonies were 50% more abundant than fragments.

Three types of thickets were identified by the agglomerative cluster analysis (Fig. 2). Underwater photographs illustrating the general appearance and extent of live coral cover typical of each of the three types of thickets are presented in Fig. 3. Group A (Coral Ridge), the most dissimilar, included the thicket with the lowest percentage of algal cover and the highest percentage of dead coral and rubble. Group B (Commercial I, Commercial II, and Dave) consisted of thickets with the highest percent coral cover (15–27%). Group C (Oakland I, Cervicornis II, and Oakland II) included those with the highest percentage of hard bottom (60–75%). The SIMPER analysis indicated that the benthic categories contributing most to the similarities among thickets were: hard bottom > live coral cover > total coral cover (live and dead) > percent algae.

Surveys conducted between July and August 2002 indicated that WBD was ubiquitous at all thickets (Table 4). Our study revealed that no bleaching was associated with any of the diseased *A. cervicornis* colonies. Thus, we infer that type I WBD was the kind prevalent at all the study thickets (see http://coral.aoml.noaa.gov/coral_disease/white_band.shtml). Except for Commercial I, WBD was present in more than 20% of all survey quadrats. The estimated percent mortality of *A. cervicornis* due to WBD was highest at Coral Ridge (7.5%), compared to all other thickets (0.1–1.4%). White band

Table 2 Summary statistics (mean % cover ± SEM) of coral community structural parameters for the seven study thickets off the coast of Fort Lauderdale, Florida, USA

Community parameter	Dave	Coral Ridge	Cervicornis II	Oakland I	Oakland II	Commercial I	Commercial II	Statistical comparisons
Live coral	27.7 ± 3.7	7.7 ± 1.2	5.5 ± 1.2	14.9 ± 3.6	10.5 ± 1.7	15.2 ± 2.7	18.6 ± 2.6	Dave > CRidge, Cerv II, Oak I, Oak II. Comm II > CRidge, Cerv II. Kruskal-Wallis, $p < 0.05$, Dunn's test
Acropora	25.9 ± 3.9	7.5 ± 1.3	5.0 ± 1.2	14.4 ± 3.5	10.0 ± 1.8	14.6 ± 2.7	16.3 ± 2.7	Dave > CRidge, Cerv II. Comm II > Cerv II. Kruskal-Wallis, $p < 0.05$, Dunn's test
Non-*Acropora*	1.8 ± 0.9	0.3 ± 0.1	0.5 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.2	1.7 ± 0.3	Dave > CRidge, Comm I, Oak I, Oak II. Comm II > CRidge, Comm I, Oak I. Cerv II > CRidge. Kruskal-Wallis, $p < 0.05$, Dunn's test
Dead coral	11.9 ± 2.7	35.9 ± 4.1	3.4 ± 0.4	1.1 ± 1.1	2.8 ± 1.3	2.2 ± 0.6	6.0 ± 1.2	CRidge > Oak I, Oak II, Comm I, Comm II, Cerv II. Dave > Oak I, Oak II, Comm I, Cerv II. Comm II > Oak I, Oak II. Kruskal-Wallis, $p < 0.05$, Dunn's test
Total coral (live + dead)	39.8 ± 4.2	44.7 ± 4.4	8.0 ± 1.8	16.2 ± 3.7	12.1 ± 2.3	15.2 ± 2.7	22.8 ± 3.2	Dave, CRidge > Oak I, Oak II, Cerv II, Comm I. Comm I > Cerv II. Kruskal-Wallis, $p < 0.05$, Dunn's test
Hard bottom with turf algae	44.5 ± 4.0	21.1 ± 2.6	63.4 ± 2.5	76.3 ± 3.7	75.2 ± 2.5	55.7 ± 3.6	60.9 ± 3.6	Oak I, Oak II > CRidge, Dave, Comm I. Dave, Cerv II, Comm I, Comm II > CRidge. Kruskal-Wallis, $p < 0.05$, Dunn's test
Macroalgae	5.0 ± 1.1	0.41 ± 0.3	5.2 ± 1.1	2.9 ± 0.9	5.6 ± 1.5	16.3 ± 3.0	7.9 ± 1.9	Comm I > Dave, CRidge, Oak I, Oak II, Cerv II. Dave, Comm II, Cerv II > CRidge, Oak I. Oak II > CRidge. 0 Kruskal-Wallis, $p < 0.05$, Dunn's test
Rubble	1.2 ± 0.8	12.3 ± 2.3	2.8 ± 0.7	0.7 ± 0.3	1.4 ± 0.3	1.0 ± 0.3	0.4 ± 0.3	CRidge, Cerv II > Dave, Comm II. Kruskal-Wallis, $p < 0.05$, Dunn's test
Sand	8.0 ± 1.4	16.5 ± 2.4	13.6 ± 2.3	2.8 ± 1.0	2.1 ± 0.3	7.5 ± 1.9	4.6 ± 1.9	CRidge, Cerv II > Oak I, Oak II, Comm II. Dave, Comm I > Oak I. Kruskal-Wallis, $p < 0.05$, Dunn's test

disease was more prevalent towards the center of the *A. cervicornis* thickets than in the periphery, where coral cover was lower. Statistical tests indicated a weak association between percent *A. cervicornis* cover and incidence of WBD (Pearson Product Moment Correlation, $r = 0.25$, $p < 0.05$).

In addition to WBD mortality, predation by *H. carunculata* was also observed at all thickets. However, the degree of predation varied greatly between them (Table 4). Only one scar was observed in 21 quadrats surveyed at Commercial II. In qualitative censuses, population densities of *H. carunculata* ranged between 18 and 86 ind. ha^{-1} ($n = 10$ censuses). These are gross estimates, since fireworms were highly cryptic and generally only visible when feeding (B. Vargas-Ángel and M. Berkle, personal observation); further studies are underway. Within the survey quadrats, fireworm scar sizes and densities ranged from 1.0–8.0 cm and 0–30 m^{-2}, respectively. Percent cover of *A. cervicornis* and the incidence of fireworm predation were weakly correlated (Pearson Product Moment Correlation, $r = 0.197$, $p < 0.05$), as was the incidence of WBD and

Table 3 Summary statistics (mean ± SEM) of *Acropora cervicornis* colony and fragment size and density at the seven study thickets off the coast of Fort Lauderdale, Florida, USA

Category	Dave	Coral Ridge	Cervicornis II	Oakland I	Oakland II	Commercial I	Commercial II	Statistical comparisons
Number of colonies m^{-2}	3.3 ± 0.4	2.5 ± 0.4	2.4 ± 0.4	1.3 ± 0.3	1.7 ± 0.2	3.0 ± 0.3	2.8 ± 0.3	Dave > Oak I; $p < 0.05$ one-way ANOVA, Tukey Test
Correlation[a] colony size vs % *A. cervicornis*	$r = 0.4$ $p < 0.05$	$r = 0.7$ $p < 0.01$	$r = 0.6$ $p < 0.01$	$r = 0.5$ $p < 0.01$	$r = 0.5$ $p < 0.01$	$r = 0.3$ $p < 0.05$	$r = 0.6$ $p < 0.01$	No statistical comparison
Number of fragments m^{-2}	0.7 ± 0.2	2.8 ± 0.4	1.4 ± 0.3	1.1 ± 0.3	1.0 ± 0.3	1.8 ± 0.4	1.6 ± 0.4	CRidge > Dave; $p < 0.05$, Kruskal Wallis, Dunn's test
Colony size (cm)	40.8 ± 3.2	14.7 ± 1.7	20.2 ± 2.0	33.2 ± 4.4	34.8 ± 3.2	22.3 ± 2.3	28.8 ± 2.2	Dave > CRidge, Cerv II, Comm II, Oak I, Oak II. Comm II > CRidge; $p < 0.05$, Kruskal Wallis, Dunn's test
Fragment size (cm)	15.7 ± 2.3	10.8 ± 0.7	10.2 ± 0.8	12.2 ± 1.6	14.7 ± 1.6	13.1 ± 1.0	11.1 ± 1.1	$p > 0.05$, Kruskal-Wallis

[a]Pearson Product Moment Correlation

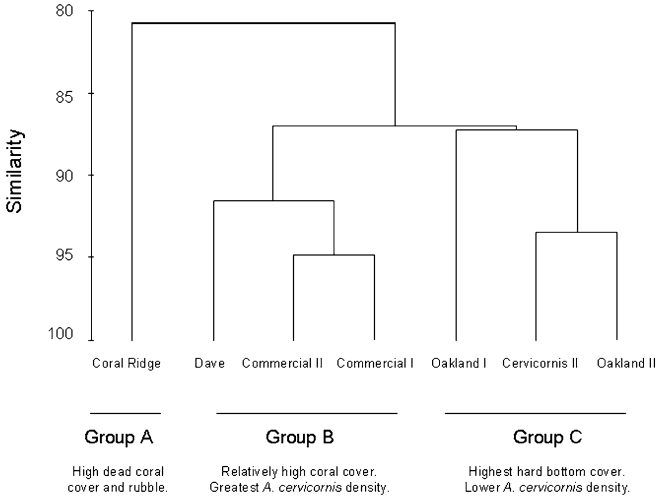

Fig. 2 Cluster analysis dendrogram of structural similarities among the study thickets based on percent cover of nine different benthic parameters (see Table 2). Similarities calculated using the Bray-Curtis similarity measure (Bray and Curtis 1957)

fireworm predation (Pearson Product Moment Correlation, $r = 0.15$, $p < 0.05$).

Discussion

Thick Caribbean Pleistocene and Holocene deposits suggest that *A. cervicornis* was an important reef-building species in the past (Macintyre 1988; Jackson 1992; Stemann and Johnson 1992). It has been suggested that during the rapid sea level rise of the Holocene transgression (10,000 to ~5,500 years before present) some *A. cervicornis* populations were extirpated as nutrient-laden waters flowed from coastal lagoons and plains into fore-reef habitats (Macintyre 1988; Fairbanks 1989; Blanchon and Shaw 1995). Nonetheless, some populations were able to survive in more favorable, protected habitats. The key to this success was probably the combination of rapid growth and asexual reproduction, via fragmentation (Tunnicliffe 1981).

Acropora cervicornis can flourish across a wide range of reef zones, depths (~5–25 m), and hydrodynamic regimes (Geister 1977; Adey 1978; Rützer and Macintyre 1982; Hubbard 1988; Aronson and Precht 2001b). In this study, thickets exhibiting the highest coral cover (group B) occurred in calmer waters (5–7 m depth), closest to shore. At these thickets, colonies attained larger sizes (up to 1.8 m diameter), and occurred in greater densities (~3 colonies m^{-2}). Although currently there is no active reef accretion at the sites examined, these study thickets developed in a habitat comparable to a back reef environment.

By contrast, thickets exhibiting high hard bottom cover (group C) occurred on the shallow (3–5 m), carbonate coquina platform, exposed to an increased hydrodynamic regime (more energetic currents and wave action), roughly comparable to a fore-reef habitat. At these thickets, colonies of *A. cervicornis* occurred interspersed with patches of hard bottom and isolated gorgonians. Here, staghorn coral colonies also attained larger diameters (up to 1.0 m) but were lower in height (< 1.0 m), with branching at seemingly lower angles. We propose that differences in colony size and morphology among the study thickets may be related to differing hydrodynamic regimes (see Veron and Pichon 1976; Bottjer 1980), which may also play a key role in determining wave-induced fragmentation, fragment retention, and hence colony densities.

The Coral Ridge thicket (group A) was unique in several aspects, despite depth and hydrodynamic regime comparable to group B. It showed the highest mean percent dead coral and coral rubble (38.2 and 14.5%, respectively). *Acropora cervicornis* accounted for most of

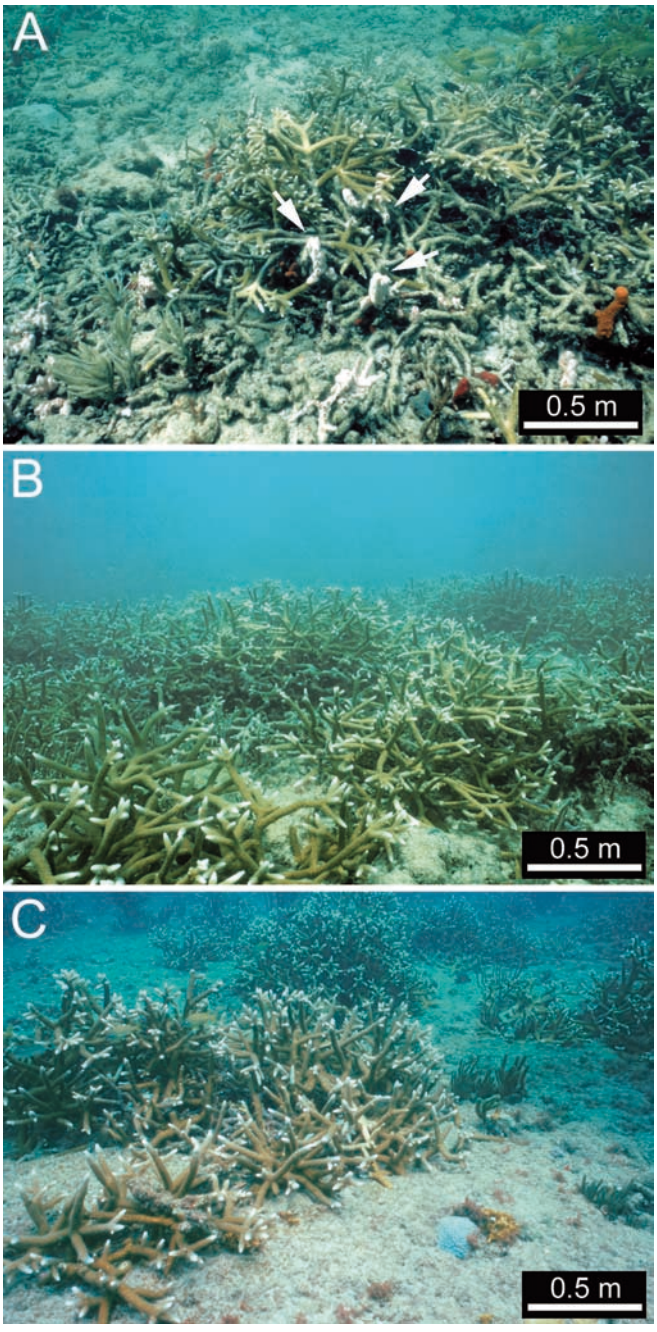

Fig. 3 Underwater photographs illustrating the general appearance and extent of live coral cover typical of the three types of *A. cervicornis* thickets identified by agglomerative cluster analysis. *Scale bars* apply to foreground. **A** Group A (Coral Ridge), note sponges (*Holopsama helwigi—white arrows*) overgrowing *A. cervicornis* and abundant dead coral and coral rubble in foreground. **B** Group B (Dave, Commercial I, Commercial II), greatest *A. cervicornis* cover and larger colonies (photo = Dave). **C** Group C (Oakland I, Cervicornis II, Oakland II), intermediate *A. cervicornis* cover and highest hard bottom cover (photo = Oakland I)

the dead coral cover and rubble, with a high percentage (~50%) of dead *A. cervicornis* in growth position. Additionally, sponges were abundant (as high as 24% cover) at the Coral Ridge thicket; several species (primarily *Holopsama helwigi* and *Iotrochota briotulata*) were observed to overgrow live and dead *A. cervicornis*.

Another interesting finding was that mean *A. cervicornis* colony size at Coral Ridge was the smallest of all study thickets (Kruskal-Wallis, Dunn's test, $p < 0.05$). This is unexpected, since extension rates for colonies of *A. cervicornis* at Coral Ridge measured by one of the authors (B. Vargas-Ángel, unpublished data) were comparable to those measured at the other study thickets, as well as those reported by Tunnicliffe (1981) elsewhere in the Caribbean. However, since extension rates show a great deal of spatial, temporal, and inter-colony variability, calcification rates may be better indicators of the coral growth responses to local environmental conditions (see Edinger et al. 2000). Smaller *A. cervicornis* colony size at Coral Ridge may reflect increased fragmentation. This was corroborated by our results, which showed that *A. cervicornis* fragment densities were >55% higher than at any of the other study thickets.

Coral Ridge was also the thicket most affected by WBD. At this thicket, 7.5% of the *A. cervicornis* cover was affected; this is over eight times higher than the overall mean for all the other thickets (0.9%). Higher incidence of WBD at Coral Ridge co-occurred with decreased colony size and higher densities of Porifera. Interestingly, reproductive studies conducted by one of the authors (Vargas-Ángel, unpublished data) during 2001–2002 showed lowered fecundity of *A. cervicornis* colonies at Coral Ridge, compared to five other thickets studied (Dave, Oakland I, Oakland II, Commercial I, and Commercial II). Decreased *A. cervicornis* fecundity at Coral Ridge results from fewer ova per mesentery and a fewer number of polyps per unit area. Studies have shown that scleractinian corals may divert resources away from sexual reproduction into other life functions in response to sublethal stress conditions (Harrison and Wallace 1990). Factors such as increased turbidity, eutrophication, thermal stress, and pollution can adversely affect coral fecundity, as well as skeletal density, bioerosion, and susceptibility to disease (Kojis and Quinn 1984; Tomascik and Sander 1987; Harrison and Wallace 1990; Edinger et al. 2000). It is possible that highly localized water quality differences due to the periodic occurrence of spin-off eddies (see Lee and Mayer 1977) may thus account for the observed differences in fragmentation, fecundity, and WBD.

Invertebrate predation can significantly impact coral populations (Turner 1994; Miller 2001). Knowlton et al. (1990) found that the impact of *H. carunculata* on *A. cervicornis* may be exacerbated when the prey species abundance is diminished due to factors such as disease and hurricanes. Furthermore, there are studies suggesting a causal link between corallivore outbreaks and disease (Knowlton et al. 1990; Antonius and Riegl 1997; Bruckner et al. 1997). Recent observations suggest that *H. carunculata* serves as a possible winter reservoir and

Table 4 Incidence of white band disease and fireworm predation (percentages and means ± SEM) at *Acropora cervicornis* study thickets off the coast of Fort Lauderdale, Florida, USA (n = number of quadrats surveyed)

Thicket	n	White band disease		Fireworm predation		
		Incidence (% of quadrats affected)	Mean % *Acropora cervicornis* affected	Incidence (% of quadrats affected)	Mean no. scars m^{-2}	Mean size of scars (cm)
Dave	32	25.0	1.0 ± 0.3	25.0	1.4 ± 0.8	4.8 ± 0.4
Coral Ridge	35	37.1	7.5 ± 1.1	17.1	0.4 ± 0.1	3.2 ± 1.3
Cervicornis II	45	22.2	1.4 ± 0.4	28.9	1.6 ± 0.5	4.4 ± 0.3
Oakland I	41	31.7	0.4 ± 0.2	29.3	0.5 ± 0.3	3.1 ± 0.3
Oakland II	17	29.4	1.9 ± 0.9	35.3	1.0 ± 0.5	4.5 ± 1.0
Commercial I	23	8.7	0.1 ± 0.1	65.2	2.3 ± 0.5	4.0 ± 0.3
Commercial II	21	23.8	0.7 ± 0.6	4.8	0.1 ± 0.1	4.0

potential vector for *Vibrio shiloi*, a bacteria known to induce coral bleaching disease in *Oculina patagonica* (Rosenberg 2002; Sussman 2002). In this study, we observed a weak association ($r = 0.25$) between the occurrence of WBD and fireworm predation. For example, the Coral Ridge thicket exhibited the highest incidence of WBD and among the lowest occurrences of fireworm predation. By contrast, at Commercial I, the mean fireworm scar density was the highest observed and WBD damage the lowest. Overall, for all thickets, fireworm predation (mean *A. cervicornis* cover affected) was six times lower than the damage attributable to WBD (mean *A. cervicornis* cover affected = 1.8%).

The potential impact of WBD on *A. cervicornis* is far greater than that of *H. carunculata*. The damage inflicted by WBD is generally irreversible, since WBD advances rapidly (Davis et al. 1986), and staghorn colonies generally cannot regenerate live tissue over exposed skeletal surfaces (except in areas exposed by breakage). By contrast, fireworm feeding scars are typically limited to branch tips, which often become overgrown by algae, bioerode, and eventually break off. Broken colony branch ends may regenerate an axial polyp and resume axial skeletal extension (personal observation). In light of the potential importance of these issues, further research is necessary.

Our results confirm prior observations that *A. cervicornis* larval recruitment rates in the field are low (see Tunnicliffe 1981; Knowlton 1992; Aronson and Precht 2001a). This result contrasts with the relatively high fecundity values (number of Stage IV ova per unit area of live coral tissue) estimated in reproductive studies by one of the authors (Vargas-Ángel et al., in preparation). Limited *A. cervicornis* larval recruitment at the study thickets may reflect lowered egg fertilization rates and egg viability due to disease, decreased substrate availability/suitability, prevailing local currents, or a combination of these factors (see Harrison and Wallace 1990). In the absence of robust "upstream" *A. cervicornis* populations in the Florida Keys, it is reasonable to assume that most of the staghorn coral recruitment observed at the study thickets may derive from local spawning events (see Vargas-Ángel and Thomas 2002). The limited larval recruitment associated with the hermaphroditic broadcast spawning mode of *A. cervicornis* may at least partly account for its failure to rebound from its recent Caribbean-wide decline (Aronson and Precht 2001a). Thus, low *A. cervicornis* recruitment rates off the coast of Fort Lauderdale, in combination with disease and potential environmental disturbances (e.g., thermal stress and hurricanes), could result in catastrophic population collapse.

The presence of *A. cervicornis* in southeast Florida is not without geological precedent. Studies by Lighty (1977) found evidence of a relict shelf-edge coral reef (at least 85 km in length), built mainly by *Acropora palmata* and *A. cervicornis* during the Holocene transgression, circa 7,000–9,000 years before present. It is presumed that as sea level rose, acroporid corals colonized shallower vacant space, migrating shoreward. Allochthonous larval supply, most likely, also contributed to seed these newly open spaces.

This study represents the first attempt to quantify *A. cervicornis* distribution and abundance off the coast of Fort Lauderdale. Thus, there are no historical baseline data to compare and assess the ecological changes of these thickets over time. Based on measurements of colony size and mean skeletal extension rates, we infer that some colonies may be ~20 years old. However, the presence of conspicuous *A. cervicornis* rubble fields within and adjacent to some study thickets (e.g., Coral Ridge, Commercial I, and Commercial II) confirms the prior occurrence of *A. cervicornis* in the region, and suggests changes in thicket spatial coverage and/or location over a longer time scale.

Conclusions

The persistence and growth of dense *A. cervicornis* thickets off the coast of Fort Lauderdale are noteworthy for several reasons:

1. These thickets represent the largest extant *A. cervicornis* population in the continental USA.
2. Overall mean live coral cover off the coast of Fort Lauderdale is low (1–7%; Goldberg 1973; Raymond and Antonius1977; Gilliam et al. 2002). Thus, the

presence of *A. cervicornis* thickets increases bottom topographic complexity, and provides habitat for numerous species of invertebrates and fishes.
3. These thickets develop in close proximity to highly urbanized coastal features and presumed attendant anthropogenic stressors, including increased freshwater discharge, coastal runoff, sedimentation, sewage effluent, nutrient enrichment, and ship traffic (Thomas et al. 2000).
4. Mortality due to white band disease and invertebrate predation appears to be relatively low in most thickets.
5. The *A. cervicornis* population off Fort Lauderdale thus provides an interesting counterpoint to the declining and disease-stricken *A. cervicornis* populations throughout the Caribbean, and especially in the Florida Keys National Marine Sanctuary.

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