

A window to the past: documenting the status of one of the last remaining ‘megapopulations’ of the threatened staghorn coral *Acropora cervicornis* in the Dominican Republic

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ABSTRACT

1. *Acropora cervicornis* (staghorn coral) and *Acropora palmata* (elkhorn coral), once common features of shallow Caribbean reefs observed growing as large stands or thickets, are now found mainly as remnant pockets or isolated colonies at a fraction of their historical areal extent.

2. In February 2010, a large, surviving population of *A. cervicornis* was surveyed at Cabezos del Cayo, Punta Rusia, Dominican Republic to document its present condition and potential threats to its persistence.

3. The *A. cervicornis* surveyed at Cabezos del Cayo provides a rare glimpse of the habitat structure that these keystone components of coral reefs once provided. The staghorn population covers an area of 2 ha and is formed by interlocking skeletons of unusually large and thick *A. cervicornis* colonies.

4. The large size of its colonies (maximum branch length 250 cm; average linear length of live tissue 471 cm; maximum number of branch tips 141 per colony; maximum branch diameter 5 cm) and the complex open canopy of these colonies, have not been described, to our knowledge, in the recent literature.

5. The site is within Montecristi National Park but there is no active protection in this area and signs of overfishing are evident based on low fish abundance and complete lack of fish >20 cm in length.

6. The stressors associated with this population include significant predation by gastropods and fireworms, overgrowth by macroalgae, damselfish ‘gardening’ activities, and white band disease.

7. The management priority for the staghorn population at Cabezos del Cayo, Dominican Republic, should be to enforce the legal framework that is already in place for the protection of Montecristi National Park, limiting unsustainable and damaging fishing practices, and limiting land-based sources of pollution associated with increasing population numbers and future coastal development.

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INTRODUCTION

The protection and recovery of coral species that have experienced drastic declines has become a focus of attention for coral reef managers and scientists. This is especially true for the Caribbean genus *Acropora*, which has undergone significant regional declines in abundance and condition that have prompted its listing as ‘threatened’ under the US Endangered Species Act (Aronson and Precht, 2001a; Precht

et al., 2002; NMFS, 2006). The factors associated with the decline of *Acropora* in the Caribbean are those identified for other species and regions, and include epizootic outbreaks (Gladfelter, 1982; Aronson and Precht, 2001b), hurricanes (Woodley *et al.*, 1981; Lirman and Fong, 1997), extreme temperature events (Jaap and Sargent, 1994), predation (Knowlton *et al.*, 1990; Miller *et al.*, 2002), and other stressors (Bruckner, 2002). The consequence of the loss of

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live tissue cover from staghorn (*Acropora cervicornis*) and elkhorn (*Acropora palmata*) colonies caused by these disturbances can extend well beyond immediate impacts. As members of one of the key reef-building genera in the region (Adey, 1978; Lighty *et al.*, 1982), reductions in live coral cover results ultimately in a loss of reef structure and associated ecological, economic, and societal services provided by this three-dimensional structure (Alvarez-Filip *et al.*, 2009; Paddock *et al.*, 2009). The tools proposed for the recovery of this genus at the local and regional levels include the establishment of marine protected areas (MPAs), controls on land-based sources of pollution, and active propagation and restoration (Bruckner and Hourigan, 2002; Miller and Szmant, 2006; Herlan and Lirman, 2009; Lirman *et al.*, 2010).

While large living stands or thickets of *Acropora* colonies were once common features of shallow Caribbean reefs (Goreau, 1959; Dustan and Halas, 1987; Aronson and Precht, 1997), remnant staghorn and elkhorn populations now appear mainly as small pockets or isolated colonies at a fraction of their historical areal coverage (Davis, 1982; Miller *et al.*, 2002, 2009). The reduction in the size of remnant living populations and the increased spatial isolation caused by the severe decline pose additional threats to the recovery of this genus by limiting sexual reproduction potential (Baums *et al.*, 2006). Thus, the discoveries of large, living populations that can be important sources of both genotypic diversity and sexually produced propagules, are infrequent but clearly positive findings for the future recovery of this genus (Vargas-Angel *et al.*, 2003; Keck *et al.*, 2005).

In 2004/2005, divers and scientists reported the sighting of a large, living population of *A. cervicornis* on the north coast of the Dominican Republic, within Montecristi National Park. Since then, this population has been visually assessed at irregular intervals but no quantitative data on its structure and status were collected. In this study, we describe the present condition of this population to establish a baseline for future change detection and to evaluate potential threats to its persistence. The site at Cabezos del Cayo, Punta Rusia, Dominican Republic, was surveyed in February 2010 using a variety of field methods aimed at documenting: (1) spatial extent of the staghorn population; (2) percentage cover of live coral tissue and macroalgae; (3) amount of live tissue, number of branches, branch diameter, height, and percentage partial mortality of staghorn colonies; (4) abundance of territorial damselfish and coral predators (i.e. gastropods, fire worms); (5) prevalence of diseases, bleaching, and coral predation; (6) abundance and species richness of reef fish; and (7) coral species richness. Key attributes of this population (e.g. colony size, tissue mortality patterns, associated fish communities) are compared with a regional database that includes more than 800 sites surveyed in the Caribbean to evaluate the comparative status of this unique and increasingly rare resource.

METHODS

Surveying large, complex populations of branching corals with interlocking skeletons poses a logistical challenge. Thicket morphology, in which one colony boundary can become indistinguishable from another often limits the surveyor's ability to assess colony-based demographic traits for *Acropora* populations. Here, we used the point-intercept method applied

to digital images of the bottom to measure percentage cover of corals and other organisms (Kohler and Gill, 2006). In addition, individual staghorn colonies were surveyed to provide information on colony sizes, tissue mortality patterns, and stressor prevalence. The demographic (i.e. colony-based) approaches to the assessment of *Acropora* stands implemented here are adapted from previous work by Vargas-Angel *et al.* (2003), Grober-Dunsmore *et al.* (2006) and Williams *et al.* (2006). These methods, complemented by fish and coral predator surveys, provide a comprehensive assessment of the status of staghorn populations and collects information on diverse baseline metrics against which future changes can be fully ascertained. The unusual morphology of the staghorn colonies (i.e. large colonies, open canopy) provided a better opportunity to track individual skeletal units and allowed for good characterization of colony-based metrics, which could have been extremely challenging in thickets with smaller colonies and very tight canopies, as shown by Vargas-Angel *et al.* (2003) in Florida and Keck *et al.* (2005) in Honduras.

The outline of the main *A. cervicornis* population was delineated, from the surface, by a snorkeler holding a GPS unit while recording a continuous track. The staghorn population has a distinct edge as dense staghorn colonies transition into sand, seagrass, or mixed communities dominated by other species, allowing for a clear determination of the patch boundaries. While isolated colonies of *A. cervicornis* were observed beyond the patch boundaries, the dense thicket aggregations were all included within the delineated boundaries. The track was used to determine the spatial extent of the population.

Sampling within the staghorn patch was conducted using 18 haphazardly deployed 10 m linear transects (depth = 4–8.5 m). All the *A. cervicornis* colonies with live tissue intersected by each line transect were surveyed to obtain the following metrics: (1) the total linear length of live tissue; (2) the percentage of the whole colony that had live tissue; (3) number of branch tips and branch tips showing signs of recent mortality; (4) maximum branch diameter (living branches only); (5) colony height estimated as the length of longest (or tallest) branch; and (6) percentage recent partial mortality. Data were averaged within transects. Individual staghorn colonies are often hard to distinguish within interlocking frameworks. However, the large size of colonies and the open canopy of the staghorn patch at Cabezos del Cayo allowed divers to distinguish (to the best of their abilities) individual colonies in this study. Individual colonies were defined as those ramets possessing a single basal attachment to the bottom. Colonies adjacent to each other that exhibited fused branches were considered as a single colony in these surveys. The total linear length of live tissue on each colony was estimated by adding up the lengths of all live branches and tissue isolates. Recent partial mortality was considered as any portion of the skeleton devoid of living tissue but still retaining calyx and skeletal structure devoid of significant algal overgrowth. This metric is included to provide an indication of tissue mortality that took place within a few months of the time of survey (Kramer and Lang, 2003). In addition to the coral metrics, the presence of urchins, corallivorous gastropods, damselfish lawns, and evidence of recent predation by the polychaete worm *Hermodice carunculata* were noted. The presence of white tips was used as a proxy for fireworm predation since these organisms, often active at night (Marsden, 1962), were

not directly observed during these day-time surveys. Lastly, the colonization of macroalgal taxa on the coral skeleton was noted for each colony.

A survey of corallivorous snails was conducted within the coral transects. In addition, roving-diver surveys (four 1 h surveys) were conducted and all snails observed were collected by hand, identified, and measured.

Digital images were collected along each transect at a distance of roughly 50 cm from the top of the coral colonies to document percentage cover of corals and macroalgae using the point-intercept method. Twelve non-overlapping images were selected along each transect and 25 random points were superimposed onto each frame as described by Kohler and Gill (2006). Each image captured roughly 0.25 m² of the bottom for a total area surveyed within each transect of approximately 3 m². The minimum number of images and points needing to be analysed were determined based on preliminary analyses conducted using methods described in detail by Brown *et al.* (2004). The benthic taxon or category immediately under each point was identified (e.g. live and dead coral, macroalgae, other organisms) and the proportional abundance (cover) was assessed for each category. Data were averaged within transects.

Twelve fish transects were surveyed (depth 4–10 m) using the Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology (Kramer and Lang, 2003). Each transect (30 m × 2 m) was visually surveyed to document abundance and sizes of all reef fish observed. Fish lengths were assigned to one of six size categories (0–5, 6–10, 11–20, 21–30, 31–40, >40 cm). Finally, a cumulative species richness count for stony corals and reef fish was performed by roving divers during five 60–90 min dives.

RESULTS

The staghorn population at Cabezos del Cayo is located on the north coast of the Dominican Republic in the Punta Rusia area (19° 52.556' N, 71° 19.847' W; Figure 1). Its longest axis is

300 m and its widest axis is 100 m. The surface area of the population is approximately 20 000 m² or 2 ha. The staghorn population appears as a semi-continuous patch of interlocking *A. cervicornis* skeletons with a limited number of other stony coral species found within the staghorn framework. The population extends from the leeward side of the shallow back-reef area of a non-emergent reef (2 m) towards shore where it reaches depths of 10–12 m. At present, live coral colonies are found at highest densities as isolated foci within the larger patch. These pockets of high live coral cover can be up to 30 m in diameter (Figure 2). In addition to these high-cover areas, live staghorn colonies (at lower densities) are scattered throughout the patch. Several areas, especially in the deepest portions of the patch, are almost completely devoid of live tissue but still exhibit the high structural complexity of live patches, suggesting a recent demise of the corals found there and limited short-term bioerosion and breakage. The distance between the tallest coral colonies and the substrate often exceeds 2 m (Figure 2).

The mean linear length of live tissue (i.e. the sum of all live branches and tissue isolates on each colony) on staghorn colonies was 335.1 cm (S.D. = ±285.8, $n = 133$ colonies). Most of the colonies surveyed were large, and mean colony height was 85.6 cm (41.7), with a maximum branch length of 250 cm. The staghorn population structure is positively skewed (i.e. fewer very large colonies), but still >25% of colonies had branches exceeding 1 m in length (Figure 3). The mean number of colonies intersected by each 10 m linear transect was 7.4 (3.6), with a minimum of two colonies and a maximum of 18 colonies per transect. The mean diameter of branches exceeded 2 cm and the largest colonies had a maximum branch diameter of 5 cm. Colony size (total linear tissue length) was significantly related to maximum branch diameter (linear regression, $r = 0.7$, $P < 0.001$, $n = 133$). The colonies also had very complex branching patterns, with a mean >20 branch tips per colony and a maximum of 141 branch tips per colony. On average, staghorn colonies had 48.6% (14.8) of their skeleton covered by live tissue. The mean percentage recent tissue mortality was 5.1% (3.4), with a maximum of 45%. Recent

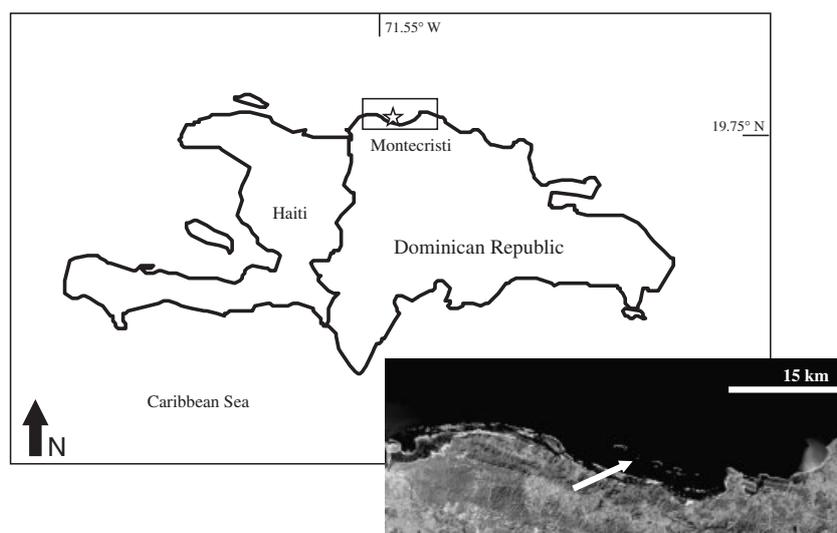


Figure 1. Map of the Dominican Republic and the location (star) of the staghorn coral population surveyed at Cabezos del Cayo. Satellite image (Landsat 7 ETM+) collected in 2002. Image processing conducted by R. Garza-Pérez and R. Ginsburg as described in Garza-Pérez and Ginsburg (2008). The white arrow points to the location of the staghorn population.

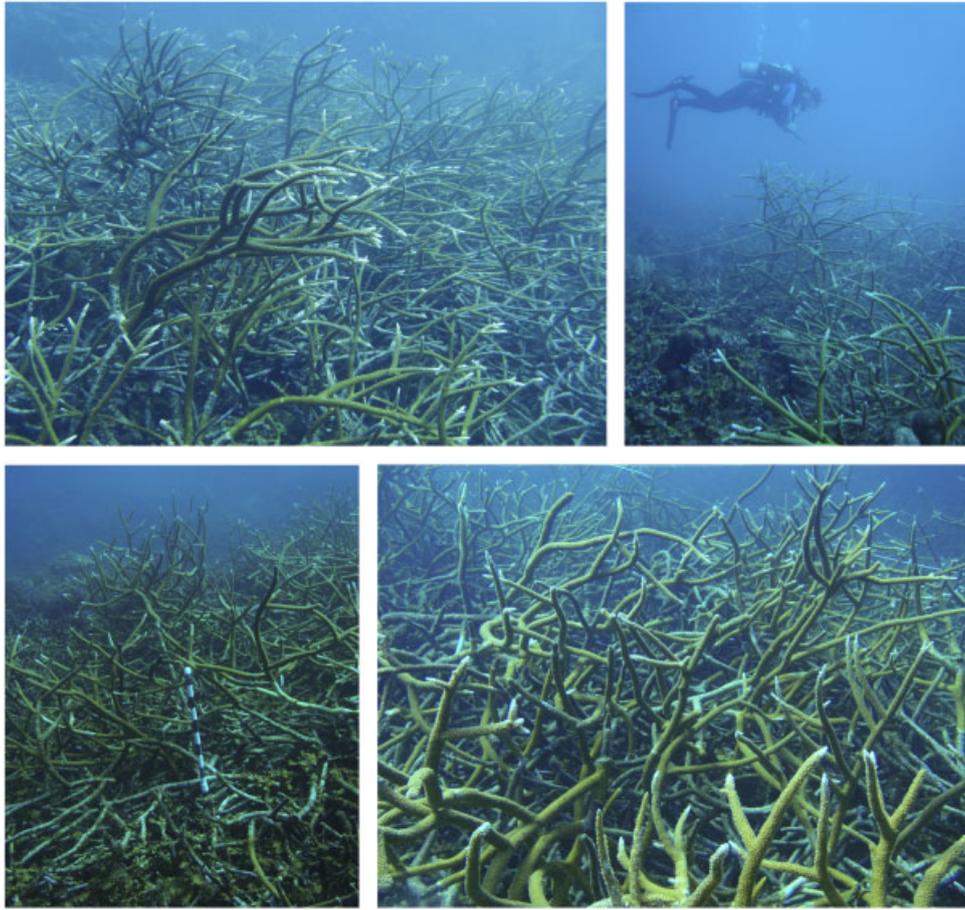


Figure 2. Photographs of the staghorn coral population at Cabezos del Cayo showing high cover and structural complexity of interlocking colonies and height of colonies that often exceeded 2 m. The PVC scale on the bottom left image is 50 cm in length.

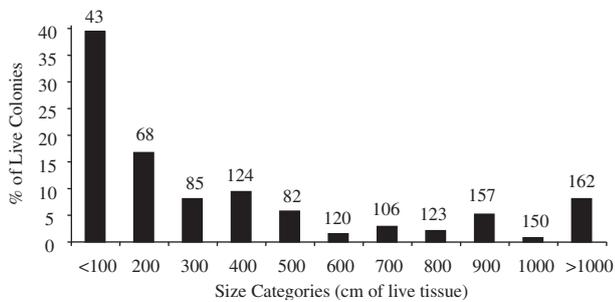


Figure 3. Frequency distribution of colony sizes (cm of live tissue) within the staghorn population. $N = 133$ colonies. Numbers appearing above the bars represent mean height of colonies (cm) within each size category.

mortality was observed at the branch tips, bases, and the middle of the branches (Figure 4). No significant relationship was found between the size of the colonies (total linear tissue length and height) and percentage recent mortality (linear regressions, $r < 0.1$, $P > 0.1$, $n = 133$).

The abundance of damselfishes (mainly three-spot damselfish, *Stegastes planifrons*, and dusky damselfish, *S. fuscus*) was high, with 30% of colonies found within damselfish territories. Predatory gastropods (*Coralliophila abbreviata*) were found on 11.3% of colonies, and evidence of fireworm (*Hermodice carunculata*) predation (i.e. tips with

recent tissue mortality) was observed on 20.3% of colonies (Figure 4). The mean abundance of the predatory snail *C. abbreviata* was 2.0 (S.D. = 3.7) snails per transect, with a maximum of 11 snails per transect. During roving diver surveys ($n = 4$ surveys, approximately 1 h each), a total of 143 *C. abbreviata* were collected. The mean size of the snails was 2.2 (0.7) cm. Evidence of white band disease was observed on 5.3% of staghorn colonies. The lower portions or 'under-canopy' of the staghorn colonies are commonly colonized by macroalgae (Figure 4). *Dictyota* was observed growing on 48% of the colonies, crustose coralline algae on 45%, and *Lobophora* on 43% of colonies. Turf (i.e. filamentous algae with canopy height < 2 cm) was observed growing on 53% of colonies. No individuals of the sea urchin *Diadema antillarum* were observed within the staghorn framework although this grazer was abundant ($> 2-3$ m²) in nearby shallow back-reef environments. A total of 28 species of stony corals were observed at Cabezos del Cayo (Table 1).

The mean percentage cover of stony corals within the staghorn patch was 17.8% (S.D. = ± 9.7), the mean cover of macroalgae was 81.5% (9.7). The mean cover of live *A. cervicornis* was 10.3% (10.4) (Figure 5). On average, staghorn corals comprised 50% (27.6) of the total coral cover within the patch (range 10–90% of the total live coral cover) (Figure 5). The dominant types of macroalgae were crustose coralline algae (mean cover 22.6% (8.5)), found commonly on the top or canopy portions of the staghorn skeletons, and

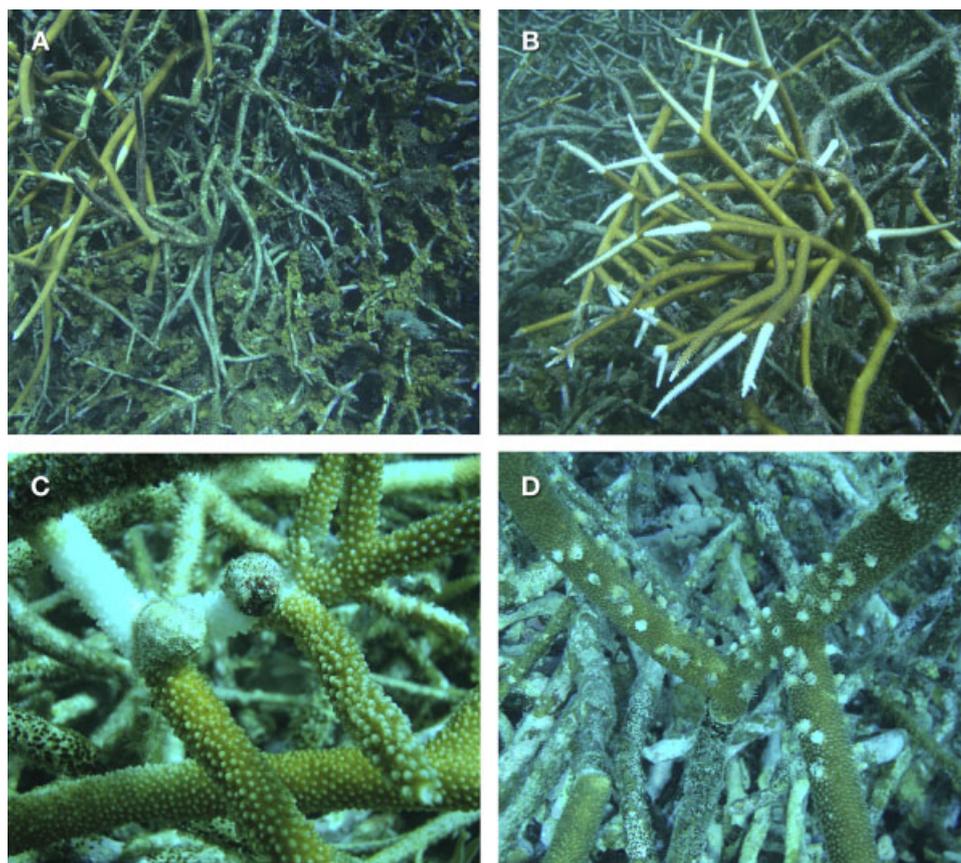


Figure 4. Stressors influencing the condition of staghorn colonies. (A) macroalgae (*Lobophora*, *Dictyota*) growing on staghorn skeletons mainly in under-story areas; (B) colonies exhibiting dead branch tips caused by the feeding activities of the polychaete worm *Hermodice carunculata*; (C) colonies exhibiting dead branch tips caused by the feeding activities of the snail *Coralliophila abbreviata* (two individuals shown in the image); and (D) tissue mortality caused by the territorial activities of damselfishes which bite coral tissue to provide substrate for macroalgae used for food and nesting.

Lobophora-Dictyota (58.9% (11.8)) that dominated the under-canopy or bottom portions of the dead staghorn colonies and framework (Figure 4).

Forty-four species of reef fish were observed at the Cabezos del Cayo staghorn population (Table 1). The reef fish community was dominated numerically by parrotfish (34% of all individuals), damselfish (28%), wrasse (25%), and surgeonfish (7%). No other taxa reached >1% of the total number of individuals observed in twelve 30 m × 2 m transects surveyed. The two most abundant species were *Scarus croicensis* (striped parrotfish; 23.6 individuals per 100 m²) and the territorial damselfish *Stegastes planifrons* (three-spot damselfish; 37.2 individuals per 100 m²). The abundance of economically important species like groupers (three individuals observed), snappers (five individuals), and grunts (two individuals) was extremely low (Figure 6). Moreover, the average size of those individuals observed was small, with just one fish (out of 1029), a trumpetfish (*Aulostomus maculatus*), >20 cm in length.

To provide a regional comparison, the data collected at Cabezos del Cayo in February 2010 were compared with similar data found in the AGRRA regional database, which contains information on coral reef status from 781 sites surveyed from 1997–2004 throughout the Caribbean (Marks, 2007). The total number of staghorn colonies within the database is 1008 (only 1.5% of stony colonies encountered) and *A. cervicornis* was found at 238 sites of the 781 sites

surveyed (30% of sites). The mean height of the staghorn colonies within the AGRRA database is 30.0 cm (S.D. = ±16.7), considerably smaller than the average colony height at Cabezos del Cayo (85.6 cm). The mean percentage recent mortality of *A. cervicornis* from the AGRRA database is 5.1% (S.D. = ±14.0), which is exactly the same value recorded for the staghorn colonies at Cabezos del Cayo. The prevalence of disease for *A. cervicornis* is 12.9% of colonies, with 11.5% of colonies exhibiting signs of white band disease (WBD) in the region compared with only 5.3% of colonies with WBD at Cabezos del Cayo. When the reef fish community at Cabezos del Cayo was compared with the regional patterns obtained from the AGRRA database (fish data were collected at 656 sites from 1997–2004), the only taxon that showed a higher abundance, compared with the regional mean, was parrotfish. All other taxa at Cabezos del Cayo had abundances lower than the regional mean (Figure 7). The parrotfish found at Cabezos del Cayo were more abundant but also smaller than the regional mean. No parrotfish >20 cm were found in the current surveys (Figure 8).

DISCUSSION

The *A. cervicornis* population surveyed at Cabezos del Cayo, Punta Rusia, Dominican Republic in February 2010 provides a rare glimpse of the habitat structure that these keystone

Table 1. List of reef fish and stony corals found at Cabezos del Cayo, Dominican Republic in February 2010

| Stony Corals | | Reef Fish | |
|----------------------------------|---------------------------------|-------------------------|--|
| Scientific Name | Scientific Name | Common name | |
| <i>Acropora cervicornis</i> | <i>Holacanthus tricolor</i> | Rock beauty | |
| <i>Agaricia agaricites</i> | <i>Chaetodon striatus</i> | Banded butterfly | |
| <i>Agaricia fragilis</i> | <i>Chaetodon capistratus</i> | Four eye butterfly | |
| <i>Agaricia lamarcki</i> | <i>Haemulon flavolineatum</i> | French grunt | |
| <i>Agaricia tenuifolia</i> | <i>Haemulon aurolineatum</i> | Tomtate | |
| <i>Colpophyllia natans</i> | <i>Scarus taeniopterus</i> | Princess parrotfish | |
| <i>Dendrogyra cylindrus</i> | <i>Scarus croicensis</i> | Striped parrotfish | |
| <i>Dichocoenia stokesii</i> | <i>Sparisoma aurofrenatum</i> | Redband parrotfish | |
| <i>Diploria labyrinthiformis</i> | <i>Sparisoma viride</i> | Stoplight parrotfish | |
| <i>Eusmilia fastigiata</i> | <i>Sparisoma chrysopterygum</i> | Redtail parrotfish | |
| <i>Favia fragum</i> | <i>Sparisoma atomarium</i> | Greenblotch parrotfish | |
| <i>Leptoseris cucullata</i> | <i>Epinephelus fulvus</i> | Coney | |
| <i>Madracis mirabilis</i> | <i>Epinephelus cruentatus</i> | Graysby | |
| <i>Manicina areolata</i> | <i>Epinephelus guttatus</i> | Redhind | |
| <i>Meandrina meandrites</i> | <i>Lutjanus apodus</i> | Schoolmaster | |
| <i>Montastraea annularis</i> | <i>Ocyurus chrysurus</i> | Yellowtail snapper | |
| <i>Montastraea cavernosa</i> | <i>Acanthurus coeruleus</i> | Blue tang | |
| <i>Montastraea faveolata</i> | <i>Acanthurus bahianus</i> | Ocean surgeonfish | |
| <i>Montastraea franksi</i> | <i>Bodianus rufus</i> | Spanish hogfish | |
| <i>Mycetophyllia danaana</i> | <i>Halichoeres garnoti</i> | Yellowhead wrasse | |
| <i>Porites astreoides</i> | <i>Thalassoma bifasciatum</i> | Bluehead wrasse | |
| <i>Porites divaricata</i> | <i>Clepticus parre</i> | Creole wrasse | |
| <i>Porites furcata</i> | <i>Cantherhines pullus</i> | Orange spotted filefish | |
| <i>Porites porites</i> | <i>Stegastes planifrons</i> | Three-spot damselfish | |
| <i>Scolymia cubensis</i> | <i>Stegastes adustus</i> | Dusky damselfish | |
| <i>Siderastrea siderea</i> | <i>Microspathodon chrysurus</i> | Yellowtail damselfish | |
| <i>Solenastrea bournoni</i> | <i>Stegastes leucostictus</i> | Beaugregory | |
| <i>Stephanocoenia intersepta</i> | <i>Chromis cyanea</i> | Blue chromis | |
| | <i>Stegastes partitus</i> | Bicolor damselfish | |
| | <i>Hypoplectrus indigo</i> | Barred hamlet | |
| | <i>Hypoplectrus puella</i> | Indigo hamlet | |
| | <i>Hypoplectrus chlorurus</i> | Yellowtail hamlet | |
| | <i>Equetus punctatus</i> | Spotted drum | |
| | <i>Aulostomus maculatus</i> | Trumpetfish | |
| | <i>Holocentrus adscensionis</i> | Squirrelfish | |
| | <i>Pseudupeneus maculatus</i> | Spotted goatfish | |
| | <i>Diodon holocanthus</i> | Balloonfish | |
| | <i>Sphyrna picudilla</i> | Southern sennet | |
| | <i>Gramma loreto</i> | Fairy basslet | |
| | <i>Gymnothorax moringa</i> | Spotted moray | |
| | <i>Canthigaster rostrata</i> | Sharpnose puffer | |
| | <i>Lactophrys triqueter</i> | Smooth trunkfish | |

components of coral reefs once provided before their well-documented regional decline. The size of this particular population (2 ha) pales in comparison with the staghorn population described by Keck *et al.* (2005) in Honduras that covers 21 ha, but the uncommon morphology of its colonies makes the Cabezos del Cayo thicket a unique resource. The large size of the colonies (maximum branch length 250 cm; average linear length of live tissue 471 cm; maximum number of branch tips 141 per colony; maximum branch diameter 5 cm) and the open canopy these colonies exhibit, have not been described, to our knowledge, in the recent literature. In fact, the average height of colonies at Cabezos del Cayo is

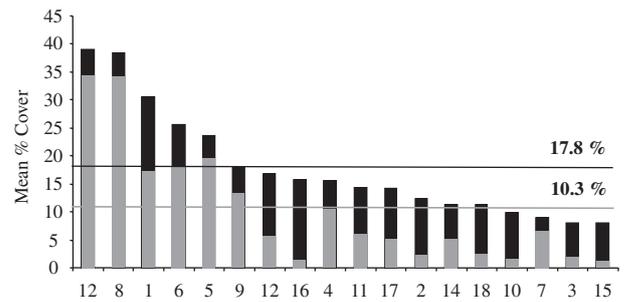


Figure 5. Mean percentage cover of staghorn (grey bars) and all corals (stacked grey and black bars) from the 18 transects surveyed in February 2010. The black line shows the global mean for all corals and the grey line shows the global mean for staghorn coral only (all transects together).

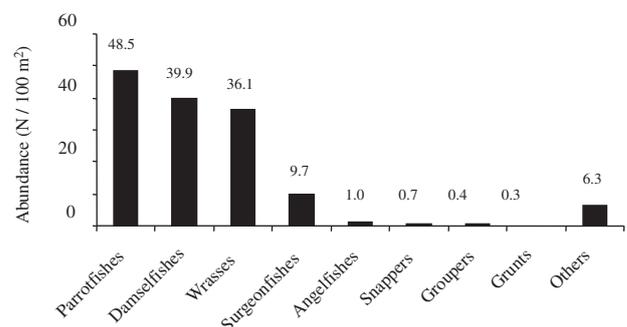


Figure 6. Total abundance of reef fishes found at Cabezos del Cayo in February 2010. Values for all 12 transects surveys are added together.

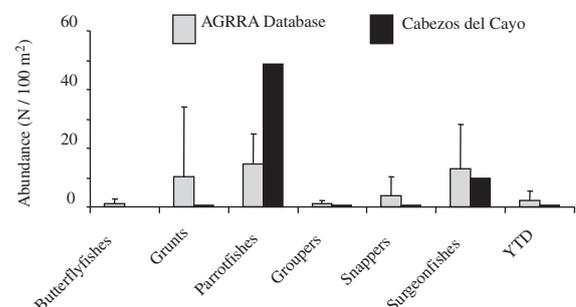


Figure 7. Abundance of reef fishes. The grey bars represent the mean abundance ($N/100 \text{ m}^2$, $\pm \text{SD}$) of the fishes surveyed using the AGRRA protocol from 656 sites throughout the Caribbean region. The black bars represent abundance values documented at the staghorn population at Cabezos del Cayo (values for all 12 transects surveys added together). YTD = yellowtail damselfish (*Microspathodon chrysurus*), only the fish that are recorded in standard AGRRA fish surveys are included here for comparison.

three times larger than the regional mean reported for this species based on surveys of more than 800 sites throughout the Caribbean (Marks, 2007). The presence of large colonies is both an indicator of favourable growth conditions over past decades as well as a high recovery potential through sexual reproduction due to the greater reproductive output of extremely large colonies (Hall and Hughes, 1996).

The stressors associated with the staghorn population at Cabezos del Cayo include predation by gastropods and polychaete worms, overgrowth by the macroalgae *Lobophora* and *Dictyota*, damselfish 'gardening' activities, and white band

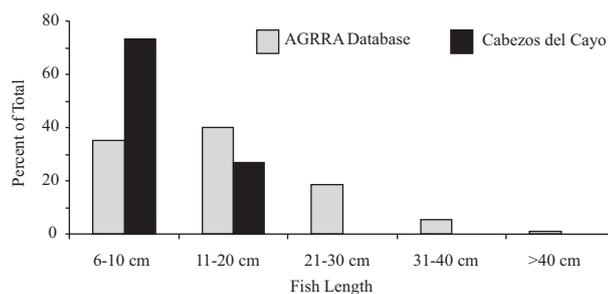


Figure 8. Size–frequency distribution of parrotfishes in the AGRRA database (grey bars) and the Cabezos del Cayo staghorn population (black bars). Juvenile parrotfishes (<6 cm) are not recorded in the AGRRA database.

disease. These disturbance factors are the same as documented for staghorn and elkhorn stands throughout the Caribbean region (Bruckner, 2002; ABRT, 2005). Prevalence of predation values at Cabezos del Cayo were similar to those recorded for staghorn populations in Florida where *Hermodice* scars were observed in up to 29% of quadrats (Vargas-Angel *et al.*, 2003) and *Coralliophila* snails were observed on 18% of colonies (Williams and Miller, 2006); and Jamaica, where a median of up to 10.5% of colonies hosted *Coralliophila* (Knowlton *et al.*, 1990). Predation is also a main source of tissue mortality for elkhorn coral, with corallivorous snails observed on 6.1% of colonies in the USVI (Grober-Dunsmore *et al.*, 2006), 18% of colonies in Puerto Rico (Bruckner *et al.*, 1997), and up to 20% of colonies in the Florida Keys (Baums *et al.*, 2003). Damselfishes, territorial fish that can kill coral tissue to grow their preferred macroalgal species for feeding and nesting purposes (Kaufman, 1977), were also identified as a key mortality factor for declining staghorn stands in Jamaica where up to a median of 25% of colonies exhibited the negative signs of damselfish activities (e.g. bites, algal lawns) (Knowlton *et al.*, 1990). White band disease, an epizootic believed to be one of the main sources of mortality to acroporid corals over the past 30 years (Aronson and Precht, 2001b), was lower in Cabezos del Cayo (5.3% of colonies affected) compared with the regional mean (11.5% of colonies) (Marks, 2007).

When the influences of all disturbance factors are combined into an integrated value of recent coral mortality, the percentage recent mortality at Cabezos del Cayo is exactly the same (5.1%) as that recorded for more than 800 sites throughout the Caribbean region (Marks, 2007). Clearly, while exposed to many of the same regional and local stressors as many other locations, staghorn thickets at this site have nevertheless shown a high level of resilience and resistance that have enabled colonies to reach unusually large size and spatial extent. Future studies, some already underway, are needed to evaluate whether water quality (e.g. low nutrients due to limited coastal development), hydrodynamics, genetics (of both the coral hosts and symbionts), or other potential factors have contributed to the survivorship and growth of this unique population.

Based on the large size of surviving colonies, it is evident that the staghorn patch at Cabezos del Cayo has escaped, for the most part, the widespread mortality patterns exhibited by most other populations in the region. However, these surveys documented the prevalence of multiple coral stressors that, if unchecked, can adversely affect the long-term persistence of this unique resource. The major sources of concern for their survivorship are the evidence of coral predation and the

detrimental territorial activities of damselfishes, which have resulted in significant tissue losses. Presently, even if most live colonies are very large by regional standards, the population size structure is positively skewed (i.e. fewer very large colonies). This may reflect a recent shift in population demography given that a high degree of structural complexity was still observed, suggesting that bioerosion and fragmentation of dead skeletons have not yet had significant time to occur. The reduction in mean colony size through partial mortality and fission resulting from compounding stressors like disease, predation, and algal overgrowth has been shown previously by Edmunds and Elahi (2007) for the coral *Montastraea annularis*, another reef-building genus that has undergone drastic regional declines.

Macroalgal overgrowth, a process involved in coral mortality around the world, should also be a source of concern for the Montecristi region of the Dominican Republic because of the low abundance and small size of herbivorous fishes. Macroalgal abundance is high (the cover of *Lobophora–Dictyota* exceeds 58%), but these taxa are presently limited mainly to the under-storey of staghorn stands where they grow on the dead bases of colonies (Figure 4). This suggests that grazing activities, except within damselfish lawns where these territorial fish exclude other grazers (Kaufman, 1977), are presently adequate, even in the absence of sea urchins and large herbivorous fish, to limit the competition between live coral tissue and macroalgal on the canopy level. However, it must be noted that the top-down control of macroalgae growth is presently possible under very low human population density and limited coastal development, which have probably limited human sources of nutrients into the coastal environment. If coastal development is increased, it is unlikely that the depauperate grazing guild can control macroalgal overgrowth and further declines in the extent and condition of staghorn populations can be expected, as shown in other areas where the combination of overfishing and increased nutrient inputs have resulted in significant coral declines (Hughes, 1994).

The establishment of marine protected areas (MPAs) has been one of the most successful management tools available for the preservation of coral reefs and other marine habitats around the world (Halpern, 2003; Lubchenco *et al.*, 2003). One of the key factors identified for the survivorship and recovery of coral populations within and around protected areas is the maintenance of an intact food web that includes both herbivores and carnivores that may control the populations of coral competitors such as macroalgae and coral predators such as *Coralliophila abbreviata* and *Hermodice carunculata* (Hughes *et al.*, 2007; Mumby *et al.*, 2007). Even if the actual beneficial mechanisms are not well understood, marine zoning has resulted in a decrease in the frequency of outbreaks of the predatory starfish *Acanthaster planci*, a major cause of coral mortality in the Great Barrier Reef (McCook *et al.*, 2010). The staghorn population at Cabezos del Cayo is located within the Montecristi National Park, created in 1983 and expanded and ratified in 2000 (Garza-Pérez and Ginsburg, 2008). However, no active management and protection of the marine resources are present in this area (Linton *et al.*, 2002), and signs of overfishing are evident from the low fish abundance and complete lack of fish >20 cm in length. The low abundance and small size of fish are similar to those found by Garza-Pérez and Ginsburg (2008) in surveys conducted in Montecristi in

2006 and in other highly exploited systems in the region (Marks, 2007). The lack of enforcement has resulted in the depletion of fish and macroinvertebrate stocks (Garza-Pérez and Ginsburg, 2008), but the small human population and limited development found in this area of the Dominican Republic seem to have provided the staghorn population at Cabezos del Cayo with a respite from other stressors of human origin, such as sedimentation, eutrophication and pollution commonly resulting from coastal development, which have all been associated with the decline in coral extent and condition in other areas of the Dominican Republic and the wider Caribbean (Linton *et al.*, 2002; Wilkinson, 2002, 2008).

Based on the evidence collected here on stress factors, it is imperative that a stricter enforcement of protection laws is enacted in Montecristi National Park to restore the trophic structure that can provide corals with increased resilience. The recovery of the overfished stocks may provide a natural control for macroalgal overgrowth by increasing the abundance of herbivores like parrotfishes that are presently harvested for food consumption, reducing the detrimental activities of territorial damselfishes by increasing the abundance of predatory fish, and potentially controlling the abundance of corallivorous organisms such as snails that have been shown to be consumed by lobsters (Johnston and Miller, 2007).

The finding of large surviving staghorn populations is clearly a positive sign at a time when reports of significant declines on reef condition and extent dominate the literature (Wilkinson, 2002, 2008). This is especially true when the coral populations described belong to the Caribbean genus *Acropora*, which has been especially hit by a number of acute and chronic disturbances that have decimated its abundance (Bruckner, 2002; ABRT, 2005). In the midst of all of the negative signs and trends, reports of unusually large or healthy *Acropora* populations such as those provided by Keck *et al.* (2005) from Honduras, Vargas-Angel *et al.* (2003) from the SE coast of Florida, USA, and the one included in this study indicate that, under the right environmental conditions, these corals are able to show vigorous growth and resilience characteristics. Nevertheless, the optimism elicited by such rare finds needs to be considered with caution as many of the stressors that have affected populations in the region (i.e. predation, high macroalgal cover, diseases) are still present and, without future management actions to preserve and restore coastal environments, may ultimately cause the all-too-familiar declining trends documented elsewhere. The management priority for the staghorn population at Cabezos del Cayo, Dominican Republic, as well as any other remnant staghorn patches that may still exist in the region, should be to enforce the legal framework that is already in place for the protection of Montecristi National Park (as also suggested by Garza-Pérez and Ginsburg, 2008), limiting unsustainable and damaging fishing practices, and limiting land-based sources of pollution associated with increasing population numbers and future coastal development.

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