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Assessing population changes of historically overexploited black corals
(Order: Antipatharia) in Cozumel, Mexico

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Abstract
Black corals (Antipatharians) play a crucial structural and ecological role on many mesophotic coral ecosystems (MCEs; reefs 30-150 m depth). In Mexico, black corals are harvested for the jewellery industry, which has historically led to populations depletion. Harvesting began in the early 1960s, and was concentrated around Cozumel Island until 1995. Here we compare populations between 1998 and 2016 for the two black coral species targeted by the jewellery industry. We found that densities of Plumapathes pennacea in 2016 are substantially lower than in 1998. However, the 2016 P. pennacea population has shifted to be dominated by larger colonies, suggesting disproportionate juvenile mortality or recruitment failure. No change in population density or colony size of Antipathes caribbeana was detected between 1998 and 2016. We advocate for the adequate protection of black corals in Mexico, and for the government to ensure sustainability of the harvesting before issuing future permits.
Introduction

Mesophotic coral ecosystems (MCEs; reefs 30-150 m depth) have gained more attention in the recent years. Still, they remain under-studied because of technical, logistical and financial challenges associated with accessing them (Hinderstein et al. 2010; Loya et al. 2016). While MCEs contain light-dependent scleractinian corals, in many cases these are not the dominant benthic taxa, with substantial structural complexity provided by other ecosystem engineers such as calcareous macroalgae, octocorals, sponges, and black corals (Antipatharians) (Kahng et al. 2010, 2014). Despite receiving some protection from threats affecting shallow reefs because of their depth (Bridge et al. 2012), MCEs are known to face threats in their own right (Andradi-Brown et al. 2016). These threats include overexploitation of economically important organisms such as fishes (Wood et al. 2006; Reed et al. 2007) and precious corals (including black corals) (Wells 1981; Wagner et al. 2012; Bruckner 2016).

Black corals are long-lived, slow growing ahermatypic corals that depend on zooplankton as their major food source (Tsounis et al. 2010; Wagner2012). About 150 black coral species (Phylum Cnidaria, Class: Anthozoa, Order: Antipatharia) have been described (Tsounis et al. 2010). Black corals occur in all oceans from shallow to abyssal depths, but are thought to be more common in tropical and subtropical regions at >50 m depths (Tsounis et al. 2010). On some MCEs, black corals are crucial habitat-forming species because of their complex structure and their ability to form dense beds which fish and other invertebrate species associate with (Boland 2005; Wagner 2012; Brucker 2016). In Hawaii, for example, Pomacanthidae and Pomacentridae fishes can be resident within individual black coral colonies, and many other fishes use black coral branches for shelter (Boland and Parrish 2005).

Black corals have slow growth rates, with annual linear growth estimates of up to 6.4 cm per year in Hawaii (Grigg 1976), and 5.1 cm per year in Jamaica (Oakley 1988).

Overexploitation of black corals for use in the jewellery industry has led to harvesting regulations in many locations (Grigg 2001; Boland 2005; Bruckner 2016). All black corals were included in the Convention on International Trade of in Endangered in Endangered Species of Wild Flora and Fauna (CITES) Appendix II in 1981 (CITES 2017).
In the Mexican Caribbean, harvesting of black corals began in the early 1960s (Kenyon 1984), and has depleted black coral populations over wide geographical areas (Padilla and Lara 2003; Padilla Souza 2004). In 1994 three black coral species were added to the Mexican national threatened species list (Padilla and Lara 2003): *Antipathes bichitoena*, *A. grandis* and *A. ules*. While species authorities were not included in the listing and taxonomy has changed, it is believed *Antipathes bichitoena* refers to *A. dichotoma* (Pallas, 1766), *A. grandis* as in Verrill (1928), and *A. ules* refers to *Myriopathes ules* (Ellis & Solander, 1786) (Padilla Souza 2004). Prior to the listing, no in-water studies of black corals had been conducted in Mexico. These three species were added in the list by international recommendation, because of concern that harvesting could lead to black coral depletion, which had been recorded in other areas (Wells 1981; Wagner 2012; Bruckner 2016). However, the inclusion of these species was a mistake, as they have not been recorded from the Mexican Caribbean or Mexican Pacific coasts, and based on their known distributions are unlikely to be found in Mexican waters (WoRMS 2004; 2008a; 2008b). Following surveys in 1998-1999, eight black coral species were recorded in the Mexican Caribbean, with the two main harvested species identified as: *Antipathes caribbeana* (Opresko 1996) and *Plumapathes pennacea* (Pallas 1766) (Padilla 2001; Padilla and Lara 2003). Despite realisation of the mistake on the Mexican protected species list, the original 1994 listing has not been updated, resulting in no national level protection for any recorded Mexican black coral species.

Cozumel, a small island off the north-eastern Yucatan peninsula, Mexico, is the major production and sales centre for the Mexican black coral jewellery and handcraft industry (Kenyon 1987; Padilla 2001). Historically, reefs around Cozumel were famed for extensive, densely populated MCE black coral beds, though these have long-since disappeared (La Torre Alegria 1979; Kenyon 1984; Humann and Deloach 2001). Harvest rates from Cozumel in the mid-1970s were between 70-121 kg gross black coral product per year (La Torre Alegria 1979). By the late 1980s and early 1990s rates had risen to between 1000-1500 kg per year, which likely caused the loss of black coral beds in the area (Padilla and Lara 2003). Official permits for commercial harvesting of black corals were first issued for Cozumel in the early
1980s. Mexican authorities suspended permission for black coral extraction in Cozumel in 1995 citing collector safety, as commercial sized colonies had reportedly been depleted to >75 m depth (La Torre Alegria 1979; Padilla Souza 2004). This resulted in collectors adopting increasingly deeper high-risk bounce diving, whereas in the past collectors could harvest colonies from as shallow as 20 m (Padilla Souza 2004).

Despite declining Cozumel black coral populations, no assessments were conducted until 1998 when extensive baseline surveys were carried out. These surveys recorded black coral densities and colony height, width and stem diameter at 15 sites on the west coast of Cozumel (Padilla 2001; Padilla and Lara 2003; Padilla Souza 2004). With no available historic data, Padilla and Lara (2003) compared the Cozumel black coral densities and sizes to remote offshore Mexican reefs. They found low black coral densities around Cozumel, suggesting that harvesting has caused a ‘serious deterioration’ of Cozumel black coral populations. While the Mexican government continues to issue permits for black coral harvesting on the Mexican Caribbean coast, since the 1995 no new permits have been issued for Cozumel. However, because of the rapid overexploitation black coral beds on mainland, harvesters have expressed interest on obtaining permits to harvest in Cozumel again (E. Gress, pers. comm.).

Here we report a new black coral population assessment conducted around Cozumel during 2016. We compare changes in the population densities and size distribution of the two historically harvested species of black coral, *A. caribbeana* and *P. pennacea*, on MCEs between 1998 and 2016 to evaluate current population trajectories and inform on-going harvesting management.

**Methods**

**Black Coral Surveys**

Surveys were conducted at eight sites on the west coast of Cozumel, Mexico during August-September 2016. Five sites were within the Cozumel National Marine Park, and three were in an area with no protection adjacent to the main town. MPA sites were Santa Rosa, Colombia, Punta Tunich, Palancar Jardines and Herradura,
and non-mpa sites were transito transbordador, purgatorio and villa blanca (figure 1).

figure 1. location of survey sites relative to cozumel and the national marine park and flora & fauna protected areas on cozumel. sites (and their gps locations in wgs84 format included in parenthesis) were: 1 – colombia (20.31497 n, 87.02625 w), 2 – herradura (20.3299 n, 87.0278 w), 3 – palancar jardines (20.33565 n, 87.02773 w), 4 – santa rosa (20.37618 n, 87.02757 w), 5 – punta tunich (20.41128 n, 87.02245 w), 6 – villa blanca (20.48913 n, 86.9721 w), 7 – transito transbordador (20.49565 n, 86.96798 w) and 8 – purgatorio (20.51578 n, 86.95383 w).
Black coral surveys were conducted using a diver-operated stereo-video system (stereo-DOV), consisting of two cameras separated by 0.8 m and with approximately 3° convergence angle filming forward along the reef. A stereo-DOV system records two synchronised images of the reef, allowing accurate length measurements of reef benthic organisms (Turner et al. 2015; Bennett et al. 2016). The stereo-DOV used two GoPro Hero 4 Black cameras and a spool system with biodegradable (100% cotton) line for measuring out each transect (see Gress et al. in review for details). Transects were 30 m in length and each separated by 10 m intervals. On each site, four transects were conducted at 55 m depth, giving 32 transects in total across all eight sites. Transects were filmed during daylight hours using natural ambient light. When filming transects, the stereo-DOV operator swam with the cameras recording forward along the reef at the 55 m depth contour while carefully looking for colonies. Upon encountering a black coral, the operator slowed and angled the cameras to ensure the coral was captured clearly on both cameras.

Permits for surveys were issued by the Comisión Nacional de Áreas Naturales Protegidas (CONANP) Cozumel, Permit Number: FOO.9.DPNAC/305-16.

We also obtained the raw Cozumel data from Padilla Souza (2004), which contains densities and colony sizes for *A. caribbeana* and *P. pennacea* from 15 sites from the west coast of Cozumel from 1998. These 1998 surveys were conducted by open-circuit divers at each site and spanned from 18–80 m depth. The area surveyed was estimated, and the height, width and depth of each black coral colony encountered was recorded (Padilla Souza 2004).

**Analysis**

Stereo-DOV footage was analysed using EventMeasure (v4.42, SeaGIS, Melbourne, Australia). All *A. caribbeana* and *P. pennacea* colonies within a 4 m transect width (constrained using EventMeasure) were identified, giving a total density for each species per 120 m² transect. The maximum height and maximum width of each colony was measured using EventMeasurement built in length measurement tools.

As the black coral density data did not meet assumptions for parametric statistics, differences in *A. caribbeana* and *P. pennacea* density between 1998 and
2016 was assessed using Mann-Whitney U tests. Changes in colony size (maximum height and maximum width) were tested using kernel density estimates (KDEs) and permutation tests, following Langlois et al. (2010). This method allows differences between two length distributions to be tested, while also providing an indication of which regions of the distributions are different if significant differences are detected. KDEs are fitted separately to the two groups with the Sheather-Jones selection procedure (Sheather and Jones 1991) using the ‘KernSmooth’ package (Wand 2013), and plotted. A permutation test then randomly allocated the data into two groups, and the mean and standard error of these randomly allocated distributions can be plotted. The permutation test was run for 9999 permutations, and used the function ‘sm.density.compare’ in the package ‘sm’ (Bowman and Azzalini 2014), in R (R Core Team 2013). As 2016 data was limited to transects at 55 m depth, while the 1998 data incorporated colonies surveyed from 18-80 m depth, we tested for changes in colony size with depth within the 1998 data using linear models. Linear model residual plots were inspected to ensure model assumptions were not violated. Permutation tests comparing changes in colony size between years were run comparing 2016 surveys with all 1998 data, and just colonies recorded between 50-60 m depth in 1998.

Results

Changes in black coral density

In 2016, a total of 28 *P. pennacea* and 15 *A. caribbeana* colonies across all 32 transects were recorded. *P. pennacea* was more abundant than *A. caribbeana* in 2016, with mean densities of $0.73 \pm 0.50$ and $0.39 \pm 0.11$ per 100 m$^2$ respectively (mean ± SE; Figure 2). Mean black coral colony density was lower for both *A. caribbeana* and *P. pennacea* in 2016 than 1998 (Figure 2). However, while this represented a significant decline for *P. pennacea* (Mann-Whitney U=107, $p=0.003$), it was not significant for *A. caribbeana* (Mann-Whitney U=69, $p=0.582$).
Figure 2. Change in black coral density between 1998 and 2016 for (A) A. caribbeana, and (B) P. pennacea. Error bars show 1 standard error above and below the mean.

We also compared 2016 black coral density between our five sites inside the Cozumel MPA and the three sites outside. A. caribbeana density was greater inside the MPA than outside Mann-Whitney U=14.5, p=0.044), with 0.58 ± 0.10 colonies per 100 m² inside the MPA compared to 0.07 ± 0.07 colonies per 100 m² outside the
MPA. There was no difference in *P. pennacea* density between sites inside the MPA and those outside (Mann-Whitney U=9, *p*=0.73).

**Changes in black coral colony size**

KDEs indicated that there was no change in *A. caribbeana* size between the two surveys, while *P. pennacea* colonies were larger in 2016 than 1998 (Figure 3). *A. caribbeana* colony height was surprisingly consistent between years, with median colony heights of 59 cm in both 1998 and 2016 (Figure 3A). *A. caribbeana* median colony width had a larger magnitude of difference, 50 cm in 1998 versus 66 cm in 2016, although this was not significant (Figure 3C). In contrast, *P. pennacea* colonies were both taller (median: 75 cm in 1998, 134 cm in 2016; Figure 3B) and wider (median: 61 cm in 1998, 105 cm in 2016; Figure 3D) in 2016.

![Figure 3](https://example.com/figure3.png)

**Figure 3.** Change in black coral colony size between 1998 and 2016, for (A) *A. caribbeana* height and (B) *P. pennacea* height.
caribbeana colony height, (B) P. pennacea colony height, (C) A. caribbeana colony width, and (D) P. pennacea colony width. Kernel density estimates were used, followed by a permutation test to identify differences between years. The grey shaded area indicates one standard error either side of the null model of no difference in colony size distribution based on year. Locations where the lines representing 1998 and 2016 are outside the grey zone indicate significant differences in the proportion of colonies of that size. n = number of colonies.

As surveys in 2016 were conducted at 55 m, whereas surveys conducted in 1998 spanned 18-80 m depth we tested for effects of depth on colony size in the 1998 data. No depth changes in colony height (F1,36=1.7, p=0.199) or width (F1,36=3.1, p=0.089) were detected for A. caribbeana. However, P. pennacea colonies were both taller (F1,215=14.8, p<0.001) and wider (F1,215=8.4, p=0.004) at shallower depths (Figure S1). Though there was high variability in colony size across this depth gradient, with low R² values of 0.06 and 0.03 for height and width respectively (Figure S1). To ensure differences identified in colony size between 1998 and 2016 were not caused by comparisons of colonies from different depths, we reran the size comparison analysis using only colonies recorded from 50-60 m depth in 1998 (Figure S2). This restricted 50-60 m depth range analysis produced results highly consistent to those using the full 1998 dataset (Figure S2; Figure 3).

To check if the change in P. pennacea colony size was caused by losing small individuals from the population, or density declines affected all sizes; we separated density data by height class. Colonies of all three-height classes (<75 cm, 75-150 cm, >150 cm) declined in density between 1998 and 2016 (Figure 4).
Figure 4. Change in black coral density between 1998 and 2016 for *P. pennacea* grouped by colony height. Stars indicate significant differences at p<0.05 using Mann-Whitney U tests. Error bars show 1 standard error above and below the mean.

**Discussion**

Results show that *P. pennacea* population densities have declined between 1998 and 2016 on MCEs around Cozumel. Colonies of *P. pennacea* identified in 2016 were larger than those recorded in 1998, but colonies of all sizes have declined in density. No significant changes in density or size were recorded for *A. caribbeana* through time; although *A. caribbeana* densities were much lower than *P. pennacea*. Unexpectedly, given the easier accessibility of shallower colonies, *P. pennacea* colonies were reported to decreased in size with increased depth in 1998.

**Differences in black coral density**

As black coral commercial harvesting has not been allowed anywhere in Cozumel since 1995, we did not anticipate any effects of the Cozumel MPA on density. Therefore, we expected the 2016 surveys to identify stable or increasing black coral populations. Results show no effect of the MPA on *P. pennacea* density, and declines across all height classes were observed between 1998 and 2016. Only
the total area of reef surveyed at each site was recorded in 1998, with no record of the area surveyed at each depth. The 1998 surveys were conducted by open-circuit technical divers, with divers quickly descending to 80 m and then slowly ascending up the reef wall to 18 m recording all colonies they encountered and trying to keep survey effort roughly equal across the depth gradient (Padilla Souza 2000, 2004). As the 1998 surveys recorded the depth of each individual colony identified, we plotted the number of colonies recorded at each depth for both species, finding the greatest frequency of *P. pennacea* colonies between 50-60 m (Figure S3). Surveys from 2016 were conducted at 55 m depth which could raise the concern that differences in density between years could be driven by natural variation in black coral colony density with depth. Although this cannot be ruled out definitively, as the highest frequency of *P. pennacea* was found in the 50-60 m depth band in 1998, we believe it is highly unlikely. In addition, Padilla and Lara (2003) states that the greatest black coral abundance for all species was observed at approximately 60 m. Therefore, as there was roughly equal sampling effort across the depth gradient, and the greatest *P. pennacea* frequency was at 50-60 m, it is likely that the overall site densities from 1998 are underestimates of *P. pennacea* density at 50-60 m. If 1998 density data was available broken down by depth, we would expect more severe declines in *P. pennacea* density than the ones detected.

Interpreting the possible influence of changing colony densities with depth on *A. caribbeana* is harder. In contrast to *P. pennacea*, the greatest 1998 colony frequency was recorded at 60-70 m (Figure S3). However, the 50-60 m depth range contained the second greatest frequency, and few colonies were encountered >70 m or <40 m (Figure S3). In a similar way to *P. pennacea*, this also suggests that 1998 *A. caribbeana* density in the 50-60 m range may have been higher than the overall site estimates. If this were the case it may be possible that *A. caribbeana* densities have declined as well through time. However, this interpretation requires caution, as we only found 15 *A. caribbeana* colonies in 2016. Low densities of *A. caribbeana* around Cozumel were previously identified in the 1998 population assessment (Padilla Souza 2004). This low density reduces statistical power, and makes comparisons less reliable, especially because of the lack of colony density broken down by depth in 1998. Low *A. caribbeana* density appears to be widespread across the Mexican
Caribbean (Padilla and Lara 2003). Similarly, a preliminary study in Honduras recorded *P. pennacea* but found no colonies of *A. caribbeana* (Guzman 1998). We detected no significant difference in *A. caribbeana* density between years. It is unclear whether results would be different if 1998 density data were available for only the 50-60 m depth range.

Understanding the potential causes of *P. pennacea* loss in Cozumel requires further work. Despite no harvesting permits issued for Cozumel since 1995, the black coral jewellery market has not moved, and Cozumel is still the major production and sales centre as of 2017. Moreover, illegal harvesting of black corals continues to be a problem around Cozumel. Recent images and videos posted on social media show divers collecting black corals from locations identifiable as Cozumel (E. Gress, pers. comm.). Whilst there is no data available on how frequently this occurs, we believe that continued illegal harvesting might contribute to the declines in *P. pennacea* density we report.

**Differences in size**

Our size distribution analysis suggests that colonies of *P. pennacea* were both taller and wider on average in 2016 than in 1998, but no changes were detected for *A. caribbeana* (Figure 3). At first glance this may suggest some *P. pennacea* colonies are recovering from the historical harvesting pressure and maturing. However, *P. pennacea* density declined across all height classes (Figure 4). This shift to larger colonies suggests juvenile colonies have been disproportionately affected by the harvesting activities. Padilla Souza (2000) reported high abundance of juvenile black corals and colonies regenerating from standing bases of previously harvested colonies in Cozumel. Disentangling possible causes for a disproportionate loss of smaller colonies in the population between 1998 and 2016 is complex, but implies reduced black coral recruitment or juvenile survival. There have been few long-term studies of black coral populations conducted, and the processes affecting black coral recruitment and juvenile survival are poorly understood (Wagner et al. 2012). In Hawaii, black coral recruitment has declined (Grigg 2004), most likely caused by overharvesting mature colonies (Grigg 2004; Tsounis et al. 2010), though competition with an invasive species might also be involved (Grigg 2004; Kahng and...
Grigg 2005). This implies that while harvesting typically targets the largest colonies (Padilla and Lara 2003), the decline in large colony density in Cozumel could be reducing juvenile recruitment rates.

Other factors on Cozumel MCEs could play a part in *P. pennacea* size distribution shifts and density declines. Black corals need hard substrate for recruitment and to firmly attach onto for growth (Wagner et al. 2012), and in the Caribbean are generally associated with steep outer reef slopes (Sanchez et al. 1998). In Cozumel, surveys down to 33 m depth in the 1980s recorded mean macroalgal cover at 25 % (Jordán Dahlgren 1988), but surveys at 55 m in 2016 recorded mean macroalgal coverage at 44 % (Gress et al. in review). If macroalgal cover has increased, it could reduce substrate availability for *P. pennacea* adjacent to unstable sediment beds had lower settlement rates (Oakley 1988). On Cozumel, shallow reef scleractinian cover has dropped from 44 % to as low as 4 % at some sites, caused by coastal development (Reyes-Bonilla et al. 2014). It is unknown if reduced availability of substrate for recruitment could also be affecting the *P. pennacea* population. If this is the case, it is unclear why no effects on *A. caribbeana* density and size distribution were observed between 1998 and 2016. However, with only 15 colonies of *A. caribbeana* identified during 2016, the lack of size distribution difference with time could be due to low statistical power. *A. caribbeana* densities were also higher inside the MPA in 2016 than at sites outside the MPA (adjacent to the main coastal development where there has been the greatest shallow reef loss). Further research is required to understand factors causing the reduced densities of *P. pennacea* colonies.

Management status

The Mexican government continues to issue commercial black coral harvesting permits stating the harvesting locations allowed. Since 1995, when harvesting permits ceased being issued for Cozumel, harvest locations on the mainland coast have changed regularly due to rapid black coral depletion (Padilla and Lara 2003). A harvesting permit is currently issued until October 2018 for locations in the southern Mexican Caribbean. However, prior to our study, no black
coral monitoring has been conducted in Mexico since 1998-1999 (Padilla Souza 2000, 2004; Padilla and Lara 2003). As all black corals are CITES Appendix II listed, the Mexican government is committed to ensure that black coral harvesting for export ‘will not be detrimental to the survival of that species’, and ‘export of specimens of any such species should be limited in order to maintain that species throughout its range at a level consistent with its role in the ecosystems’ (CITES 2017). Yet, harvest areas are currently designated based on diver and industry requests following harvest depletion, rather than harvest sustainability (Padilla and Lara 2003). The CITES Trade database (trade.cites.org) contains Mexican black coral export records for the jewellery industry up to 2016, although the quantity of black coral items reported can be as low as 1 per year. These low number or reports might be because the major market for the jewellery in Cozumel is sales to tourists, who are unlikely to obtain CITES export permits, rather than large commercial exports for sale internationally. With no black coral population assessments conducted since 1998-1999, and no studies on recruitment rates or any other biological and ecological traits, it is unclear how the Mexican government is currently evaluating sustainability to continue issuing harvest permits and CITES export permits.

Moving forward, we recommend three key steps to improve protection for black corals in the Mexican Caribbean: Firstly, the Mexican threatened species list should be updated to correctly list the eight species of black coral known from the Mexican Caribbean, while acknowledging the outstanding harvesting permit. This will have several results: Primarily, it will require an increased evidence base before harvesting permits can be issued. It will also make illegal harvesting of black corals a more serious criminal offence. In addition, adding these targeted black coral species to the Mexican threatened species list will also force a review of the legal status of the existing harvesting permits. As other well-managed black coral fisheries have struggled to maintain long-term sustainability (Tsounis et al. 2010; Bruckner 2016), there is an urgent need to evaluate the biological and economic sustainability of the industry. Evidence from the few available reports show that unregulated and uninformed harvesting of black corals have quickly lead to overexploitation and population depletion in many areas in the Caribbean (Bruckner 2016). Secondly, the Mexican government has recently announced a large MPA that includes most of the
Mexican Caribbean. We strongly recommend that consideration is given to protect MCEs and their ecosystem engineers, such as black corals. Thirdly, we also encourage urgent research to understand drivers of black coral population decline both within Cozumel and the Mexican Caribbean, but also the wider western Atlantic region.

**Conclusion**

We surveyed black coral populations around Cozumel finding severe declines in density between 1998 and 2016 for the historically most abundant species, *P. pennacea*. These declines affected corals of all size classes, though appeared to disproportionately affect smaller colonies. Based on these trends, we suggest the updating of the existing legal status of black corals. We highlight the urgent need to assess the potential of biological and economical sustainability of black corals harvesting.

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Figure S1. Differences in *P. pennacea* colony (A) height and (B) width with depth from the 1998 surveys. Solid red line shows linear model, while the dashed red lines show 95% prediction intervals. *P. pennacea* colonies were both taller ($F_{1,215}=14.8$, $p<0.001$) and wider ($F_{1,215}=8.4$, $p=0.004$) at shallower depths, though $R^2$ values were 0.06 and 0.03 for height and width respectively.
Figure S2. Change in black coral colony size between 1998 and 2016, using only colonies recorded between 50-60 m depth in 1998. (A) *A. caribbeana* colony height, (B) *P. pennacea* colony height, (C) *A. caribbeana* colony width, and (D) *P. pennacea* colony width. Kernel density estimates were used, followed by a permutation test to identify differences between years. The grey shaded area indicates one standard error either side of the null model of no difference in colony size distribution based on year. Locations where the lines representing 1998 and 2016 are outside the grey zone indicate significant differences in the proportion of colonies of that size. 

\(n=\)number of colonies.
Figure S3. Frequency distribution showing the number of black coral colonies recorded in 1998 in 10 m across the depth gradient for (A) *A. caribbeana*, and (B) *P. pennacea*. Survey effort was approximately equal at different depths in 1998 (Padilla Souza 2000; 2004).