

UNIVERSITY OF MIAMI

EXAMINING STRUCTURAL AND MECHANICAL PROPERTIES OF THE THREATENED
CORAL *ACROPROA CERVICORNIS*: EFFECTS OF NURSERY GROW-OUT PLATFORMS
ON MECHANICAL STRENGTH

By

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Examining structural and mechanical properties of the threatened coral *Acropora cervicornis*:
Effects of nursery grow-out platforms on mechanical strength

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Abstract

Reef rugosity has been severely degraded along the Florida Reef Tract (FRT) leading to the loss of key ecological services that protect the Florida coastline. Coral restoration may mitigate the decline of coral populations and restore ecosystem services of previously degraded reefs. A restored reef may be more effective at attenuating wave energy if the outplanted coral stock is itself resistant to physical disturbance. This resistance may be tied to the plastic growth phase of coral fragments in offshore nurseries which primarily employ “tree” structures floating in the water column and “block” structures attached to the substrate. Here, we conduct a mechanical analysis of nursery raised fragments to investigate the differences between the two grow-out platforms in mechanical strength. Corals grown on blocks were on average 35% more dense and 42% less porous than corals grown on trees. These skeletal characteristics increased the compressive strength of block-reared corals by 99% and increased the flexural strength by 72% when compared to tree-reared corals. The increased mechanical strength may decrease branch fragmentation in block-reared corals but may not reduce whole-colony fragmentation as the strength of the hardbottom substrate was determined to influence whole-colony dislodgement in previous studies. Therefore, we recommend that restoration practitioners focus on mitigating boring species and implement outplanting methodologies that increase the bond strength of the coral and hardbottom substrate to decrease whole-colony fragmentation in high energy environments before focusing on implementing block structures in nurseries.

1.0 Introduction

Worldwide, coral reefs are experiencing widespread degradation from a host of stressors, both natural and anthropogenic. Threats on a global scale include climate-driven ocean acidification and recurrent bleaching events from rising sea temperatures (Hoegh-Guldberg et al. 2007; Hughes et al. 2017). Reefs also face localized threats in the form of temperature anomalies (Lirman et al. 2011), physical disturbances (Madin & Conolly 2006), eutrophication (Bruno et al. 2003), disease (Miller et al. 2009), and dredging (Cunning et al. 2019), all of which compound coral stress and reduce coral resilience to bleaching (Carilli et al. 2009). In the Caribbean region and along the Florida Reef Tract (FRT), carbonate production on coral reefs is about half of that of historical (mid- to late-Holocene) production levels (Perry et al. 2013). This decline is due in part to the loss of the once-dominant reef-building *Acroporid* spp., staghorn (*A. cervicornis*) and elkhorn (*A. palmata*), which were previously decimated by bacterial white-band disease and physical disturbance from hurricanes (Aronson & Precht 2001). As a result, there has been a region-wide loss of reef rugosity (architectural complexity) leading to the loss of ecological services that protect the South Florida coastline (Alvarez-Filip et al 2009, Kuffner et al. 2019).

Coral reef lined shores throughout the world are threatened by increased coastal hazards with the coupled degradation of coral reefs and increased intensity and frequency of tropical storms. In the Seychelles, coral mortality on the reef flats and subsequent loss of reef rugosity has permitted increased wave energy to reach shores that had previously been protected by architecturally complex reefs (Sheppard et al. 2005). In the Virgin Islands, modeling suggests that the reefs present add a net benefit of approximately 8.9 million USD annually in coastal hazard reduction from 100-year return period storm event (van Zanten et al. 2014). In South Florida, with a larger coastal population and increased coastal assets, the afforded protections are

markedly greater. The FRT annually protects \$600 million in economic land assets, promotes nearly \$3.4 billion in tourism and recreation driven revenue, and supports over 36,000 jobs in South Florida (Gorstein et al. 2016, Storlazzi et al. 2019). The loss of reef rugosity along the FRT threatens to weaken the ability of these reefs to protect the South Florida coastline and its assets during future hydrodynamic disturbances. Therefore, coral reef managers have turned to coral restoration to augment conservation efforts in order to protect both the ecological function and ecosystem services of coral reefs.

1.1 Coral restoration

For over two decades, active coral restoration has become a means to rehabilitate degraded reefs using the ‘Coral Gardening’ approach (Rinkevich 1995). In this methodology, fragments from wild colonies are transplanted to a nursery and allowed to grow. Nursery-reared corals are then fragmented and transplanted back onto the reef, increasing the overall biomass and coral cover of previously degraded reefs (Johnson et al. 2011). Today, these restoration efforts have reached ecologically significant scales and are employed throughout the Caribbean, Indo-Pacific, and Australia using a myriad of methodologies (Schopmeyer et al. 2017, Boström-Einarsson et al. 2020).

Globally, healthy coral reefs attenuate an average of 97% of wave energy and can be more cost effective than artificial structures (Ferrario et al. 2014). Restoration practitioners, therefore, are now looking towards reef restoration to enhance coastal resilience while also restoring the ecological function of the reefs (Reguero et al. 2018). Lab testing in the University of Miami’s Surge Structure Atmosphere Interaction Facility (SUSTAIN) facility has showed that both wave height and energy were reduced after a model restored coral thicket, supporting the efficacy of reef restoration to mitigate coastal hazard risks (Ghiasian et al. 2019).

We hypothesize that a restored reef may be a more effective attenuator of wave energy if the outplanted coral stock is itself resistant to physical disturbance. In the ‘Coral Gardening’ method of restoration using *A. cervicornis*, this resistance may be tied to the growth phase of coral fragments in offshore nurseries, which primarily utilizes two types of coral grow-out platforms: “tree” structures floating in the water column and “block” structures attached to the bottom (Johnson et al. 2011; Fig. 1). Previous research by O’Donnel et al. (2017) and Kuffner et al. (2017) highlighted the plastic morphology of *A. cervicornis* skeletons and demonstrated that fragments grown on block structures had significantly higher skeletal density and lower linear extension rates compared to corals grown on tree structures. O’Donnel et al. (2017) hypothesized that corals grown on blocks allocated calcification resources to create a fortified, dense skeletal morphology to counteract water flow on the stationary platforms, while corals attached to trees suspended in the water column moved freely with the flow and thus allocated calcification resources to linear extension to increase its surface area and house more photosynthetic symbionts. The growth phase of the corals in restoration nurseries therefore plays an important part in shaping the structural properties of the coral skeleton (Kuffner et al. 2017).

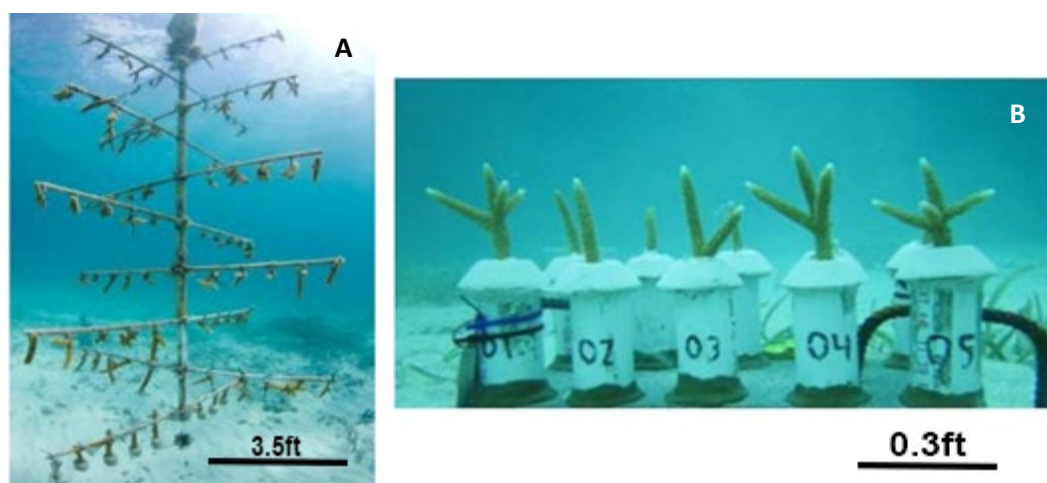


Fig. 1. Comparison of coral restoration grow-out structures: (A) mid-water floating “trees” and (B) bottom-attached “blocks”.

1.2 Structural and mechanical characteristics of *A. cervicornis*

A. cervicornis is a branching coral that grows by extending existing axial corallites and generating new axial corallites, permitting higher growth rates relative to other species, and allowing corals to compete for space and light with other species on the reef (Tunnicliffe 1981). This same growth characteristic increases the species' susceptibility to hydrodynamic disturbances since newly generated axial tips are porous and structurally weak (Tunnicliffe 1981). The bulk density, compressive strength, tensile strength, and elastic modulus (resistance to elastic deformation) of coral skeletons describe its mechanical strength and along with geometric morphology and growth direction of branches describe a colony's resistance to wave loading (Schumacher & Plewka 1981). Previous determinations of these structural characteristics of *Acroporids* are compiled in Table 1.

Table 1. Compilation of mechanical strength testing of *Acroporids*

Study	Coral Species	Density (g/cm ³)	Porosity (%)	Compressive Strength (MPa)	Tensile Strength (MPa)	Elastic Modulus (GPa)
Chamberlain (1978)	<i>A. palmata</i>	-	30	21-81	-	9-38
Vosburgh (1982)	<i>A. reticulata</i>	-	-	62-90	10.3-40.9	25-82
Baldock et al. (2014)	<i>A. intermedia</i>	2.42	12-40	28-99	8.8-12.7	55-77
Masa (2018)	<i>A. cervicornis</i>	-	-	12-38	-	-

Branching corals experience compressive and bending stress as a result of wave loading (Fig. 2). The branching morphology of staghorn corals, characterized by a high length-to-diameter ratio, is more susceptible to bending stress generated from waves than other massive coral morphologies (Vosburgh 1982, Madin 2005). As such, values derived from flexural testing are applicable in understanding wave loads required to reach structural failure.

In this study, we characterized the different mechanical properties of multiple distinct genotypes of nursery-reared *A. cervicornis* grown in two different platforms by comparing porosity, bulk density, compressive strength, and bending strength to better understand the role of different coral restoration techniques on coral outplant resilience and shoreline protection. The aim of this study is to inform restoration practitioners who seek to restore reefs with the primary goal of protecting coastlines by quantifying structural properties related to the growth of *A. cervicornis* on nursery structures. We hypothesize that the denser and less porous morphology of corals grown on block structures will have increased mechanical strength, thereby enhancing the persistence of restored staghorn populations and maximizing the protective benefits of restored reefs for coastal communities.

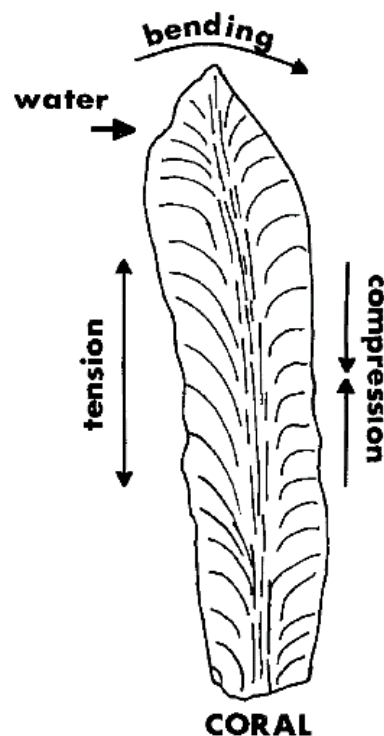


Fig. 2 Forces on coral Diagram of a branching coral demonstrates its structural grain from vertical axialite accretion shown by dark lines and the forces acting on the coral indicated by arrows denoting the direction of forces due to perpendicular waves. Reproduced from Chamberlain (1978).

2.0 Methods

2.1 Collection and preparation of fragments

Branches of large *A. cervicornis* (> 20cm total-linear-extension) grown on tree structures in the nursery for at least one year were collected from two offshore nurseries located near Key Biscayne (25.6763° N 80.0987° W) and within Biscayne National Park (25.4744° N 80.1286° W). Branches grown on block structures of similar size were collected during the decommissioning of the South Nursery also within Biscayne National Park (25.3628° N 80.1666° W) in Miami-Dade County, Florida (Fig. 4). Corals from different growth structures were unable to be sourced from the same nursery due to the lack of nursery and growth platform overlap. Colonies were of similar size to those that would be selected for outplanting, and therefore provide an accurate assessment to the hydrodynamic loads experienced by outplanted corals. For our first experiment, coral fragments approximately 5-10cm in length were selected from the core of each colony furthest from the axial tip (Fig. 3). Fragments were collected from both block (n = 48) and tree nursery grow-out platforms (n = 21). A second experiment was conducted to evaluate the influence of genotype on skeletal attributes. For this experiment, we collected fragments (n = 4 per genet) from 7 different genotypes grown on trees.



Fig. 3 A fragment of *A. cervicornis* was cut from a parent colony in the nursery and was later prepared for mechanical testing.



Fig. 4 Map of Restoration Nurseries in Miami-Dade County Corals were collected from three of the Lirman Benthic Ecology and Coral Restoration Lab nurseries within Miami-Dade county.

Coral samples were submerged in 15% diluted solution of hydrogen peroxide at a pH of 8.4 for 48 hours to completely dissolve tissue. Fragments were then rinsed with deionized water and submerged in saltwater for 72 hours to become saturated in saltwater medium prior to buoyant weight measurements. Following buoyant weight measurements, fragments were dried for 48 hours at 50°C and weighed with a precision balance to determine dry mass. Because corals lack substantial organic material within their skeletons (<0.5% by volume), dried dead samples cleaned in a diluted hydrogen peroxide solution are representative of living corals (Chamberlain 1978).

2.2 Measurement of density and porosity

A buoyant weight technique based on the Archimedean principle was used to measure the bulk volume (V_B) defined as the total volume occupied by the coral skeleton, the bulk density

(D_B) defined as the ratio of the dry mass to the bulk volume, and the connected porosity (P_A) defined as the ratio of the pore volume connected to the external surface to the bulk volume. (Jokiel et al. 1978, Fantazzini et al. 2015). Buoyant weight methodologies were performed using a precision balance where measurements could be performed both above and below the scale with a metal hook suspended on a tungsten wire in a tub of saltwater with known temperature and salinity using the following equations reproduced from Fantazzini et al. 2015:

$$\text{Bulk Volume } (V_B) = \frac{m_W - m_B}{\rho_W} \quad (1)$$

$$\text{Porosity Volume } (V_P) = \frac{m_W - m}{\rho_W} \quad (2)$$

$$\text{Bulk Density } (D_B) = \frac{m}{V_B} \quad (3)$$

$$\text{Connected porosity } (P_A) = \frac{V_P}{V_B} = \frac{m_W - m}{m_W - m_B} \quad (4)$$

where m is the dry mass, m_W is the wet weight, m_B is the buoyant weight, and ρ_W is the density of the saltwater calculated from the precise temperature and salinity of the saltwater bath.

It is important to note that only pores connected with the external surface can be saturated with water, therefore the determination of porosity using the buoyant weight technique does not include pores that are not connected to the external surface (occluded pores). However, Fantazzini et al. (2015) estimated the occluded porosity based on assumptions related to the features of the biomaterial, composed by aragonite and organic matrix and compared these estimations to Fantazzini et al. (2013) which directly measured the occluded porosity using Time-Domain Nuclear Magnetic Resonance (TD-NMR) relaxometry and mercury injection porosimetry. Fantazzini concluded that the occluded porosity was approximately 3-4% and had pore sizes less than 1 μm which were negligible in relation to the rest of the sample. Following the assumptions of Fantazzini, estimates of the occluded porosity of block-reared *A. cervicornis* have a median value of approximately 3.5% while estimates of the occluded porosity of tree-

reared *A. cervicornis* have a median value of approximately 5.5%, and therefore the occluded porosity of the collected *A. cervicornis* is deemed negligible.

2.3 Determining structural strength of skeletons

Testing of mechanical properties of corals was carried out using an Instron universal testing machine. The corals were tested in two different configurations to obtain the compressive and flexural strength. Fragments selected for mechanical testing had no signs of boring and were selected for a uniform cross-section without knots or branching along the length of the sample. Corals were cut to the desired length using a dry saw.

2.3.1 Compression Tests

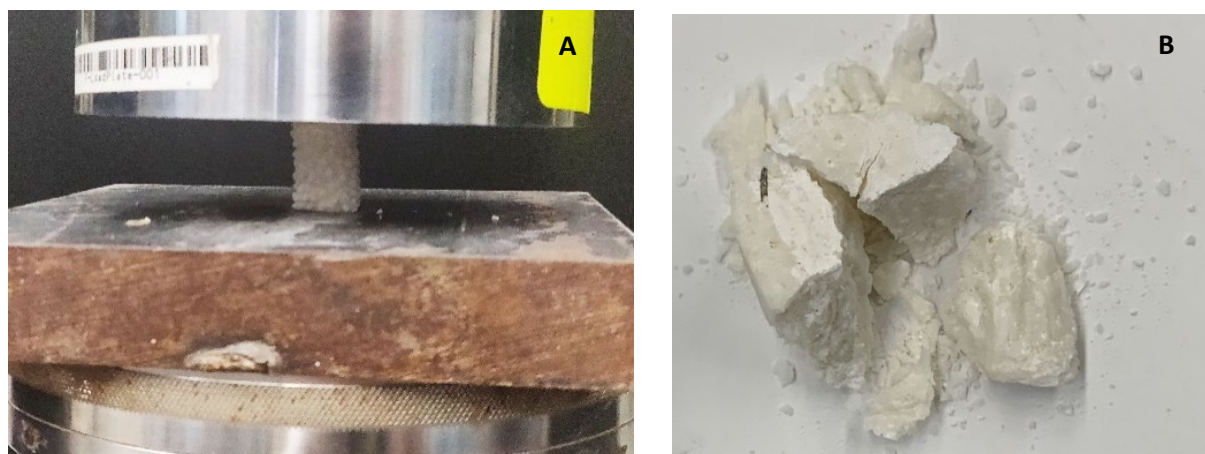


Fig. 5 Compression Test Compressive testing was used to determine the ultimate compressive strength of the block and tree raised corals. **(A)** Compression head applied a load on the sample until failure. **(B)** Fragments observed broke into shards at roughly 120 degree angles.

Compressive testing was performed on 34 samples (“tree” $n = 10$, “block” $n = 24$) to determine the ultimate compressive strength of *A. cervicornis*. Fragments were cut to a length-to-diameter (L/D) ratio of approximately 0.75 (small aspect ratio) and 1.50 (large aspect ratio) but varied within the range 0.63-1.85 due to the variability of samples. Fragment lengths (L) ranged from 12.6 to 30.6 mm and diameters (D) ranged from 13.3 to 29.7 mm. The samples were sanded

with fine grit sandpaper to ensure a uniform, smooth interface with the compression heads. This technique of fragment preparation was adapted from Masa (2018) where they used fine grit silicon-carbide sandpaper to polish samples. A compressive load was applied in displacement control mode at a rate of 0.2mm/min until failure was observed (Fig. 6) or for a period of ten minutes, whichever was earlier. The axial load-displacement (N- Δ) response was recorded by the software (and later exported) and the failure mechanism was recorded by visual observation of photographs taken for each test sample before and after testing. The ultimate compressive strength, σ_c , was obtained as the stress at failure.

$$\sigma_c = \frac{N}{\pi R^2} \quad (5)$$

where N is the load at failure, and R is the radius of the fragment.

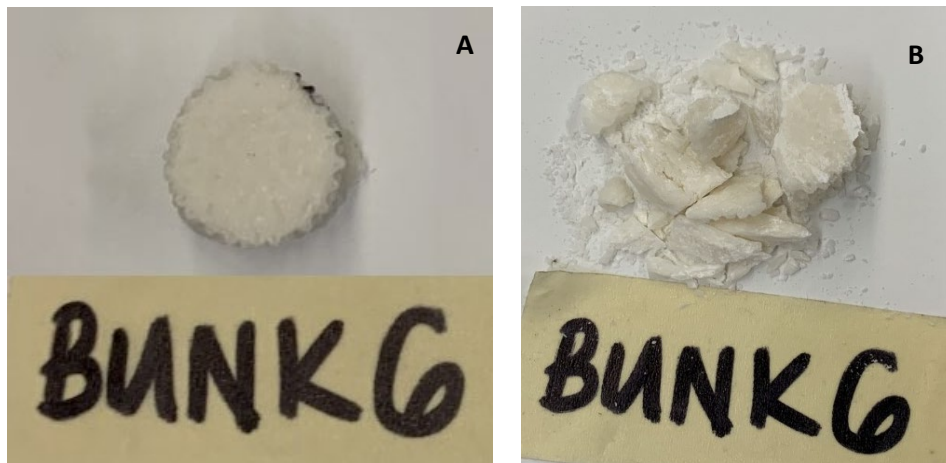


Fig. 6 Compression Testing Before and After Compressive testing of a block-reared coral (A) before and (B) after compressive testing. Fracturing patterns were consistent amongst block and tree reared corals.

2.3.2 Flexural Testing

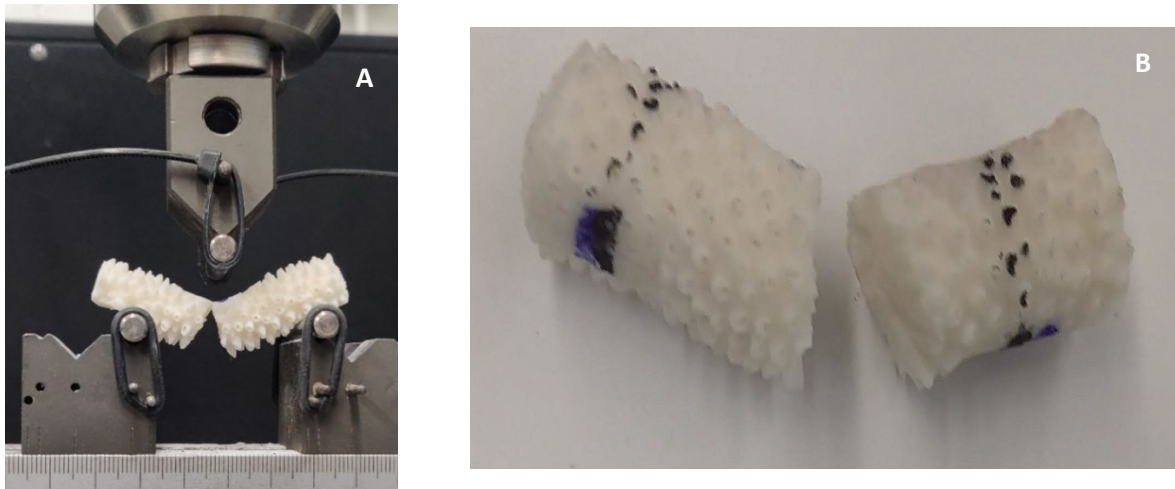


Fig. 7 Flexural Testing Flexural testing was used to determine the bending strength of coral skeletons. **(A)** A 3-point bending configuration was used to apply a load at the midpoint of the fragment until failure. **(B)** Samples were observed to fail in a uniformly flat pattern close to the midpoint consistent with other testing.

Flexural testing was performed on 23 samples (“tree” $n = 9$, “block” $n = 14$) to determine the bending strength of *A. cervicornis*. A 3-point bending configuration was adapted from ASTM D790 (ASTM 2017). The span lengths were generally maintained at 45 mm with some exceptions due to the knots on the coral. The variation of span length was ± 5 mm. The sample diameters ranged from 13 to 22.85 mm, indicating the extent of variability in coral growth between the two nursery structures. The ends of the corals and the midspan point were polished with a Dremel tool to ensure a smooth surface for seating the coral on the supports. The samples were marked at the midspan and at the location of the knife edge supports with a permanent marker to ensure the load cell was properly aligned. The load was applied in displacement control mode at a rate of 0.02 mm/min until failure (Fig. 7B) and the load–displacement ($N-\Delta$) responses were recorded. The bending strength at midspan of the specimen, σ_T , is calculated using the maximum load N obtained from the flexural test.

$$\sigma_T = \frac{N \times L}{\pi R^3} \quad (6)$$

where N is the maximum applied load, R is the radius, and L is the span of the fragment.

2.3.3 Calculations of maximum sustained flow velocities

Branching corals, with a high length to diameter ratio, are dominated by drag forces and experience negligible inertia forces. Thus, the maximum internal bending stresses acting on a branching coral can be simply modeled as a function of maximum wave induced velocity by the following equation:

$$\sigma_{max} = \frac{8\rho_w u_{max}^2 (\frac{L}{D})^2 C_D}{\pi} \quad (7)$$

where σ_{max} is the calculated peak bending stress, ρ_w is the density of water (approximately 1030 kg/m³), u_{max} is the maximum water induced velocity sustained by a passing wave, L/D is the length to diameter ratio of the fragment taken as 7 to model a representative outplanted fragment with a span of 100mm and a diameter of approximately 15cm, and C_D is the drag coefficient which is approximately equal to 1 for a cylinder over the approximate range of Reynolds numbers encountered by corals on the reef (Gerhart et al. 1992). This model assumes the geometry of each branch is a cylinder. Peak bending stress was calculated for a range of flow velocities from 1-5m/s which correspond to expected daily maximum on a typical 1–3 m deep reef platform and to that which would be expected during a tropical cyclone, respectively (Madin 2004).

2.4 Analysis

Two-sample Student's t-tests were used to compare skeletal response and mechanical strength between the two grow-out platforms. A one-way ANOVA was conducted to compare the effect of genotype on porosity and bulk density in corals grown on trees. Additionally, a Pearson correlation test was conducted to determine if mechanical strength was correlated with porosity and diameter. The data met the assumptions of the Student's t-test and ANOVA model

including normality of residuals and homogeneity of variance. When the assumption of equal variance in flexural strength was not met, a Welch's two-sample t-test and Spearman's rank correlation test assuming unequal variance were conducted instead. All statistical analyses were performed in R (v. 3.6.1) using RStudio (v. 1.2.5019) with the ggplot2 and Rmisc packages.

3.0 Results

The platform used to grow staghorn corals at the nurseries had a significant influence on the skeletal structure of the corals sampled. Corals grown on blocks had an average diameter greater than that of corals grown on trees for corals tested in flexural testing (mean \pm SD for blocks = 17.96 ± 3.26 mm, $n=14$; trees = 15.28 ± 1.64 mm, $n=9$; two-sample t test: $t=2.2708$; $p<0.05$). Block-reared corals were additionally significantly denser (blocks= 2.11 ± 0.23 g/cm³, $n=48$; trees = 1.56 ± 0.18 g/cm³, $n=54$; two-sample t test: $t = 13.535$, $p<.001$; Fig. 8A) and less porous (blocks = 23.45 ± 8.03 %, $n=48$; trees = 40.22 ± 7.12 %, $n=54$; two-sample t test: $t=11.179$, $p<.001$; Fig. 8B) than tree-reared corals. There was no significant effect of genotype on skeletal response among the genotypes grown on trees [Bulk Density: $F(6,26) = 1.016$, $p = 0.437$; Porosity: $F(6,26) = 1.479$, $p=0.224$; Fig. 9].

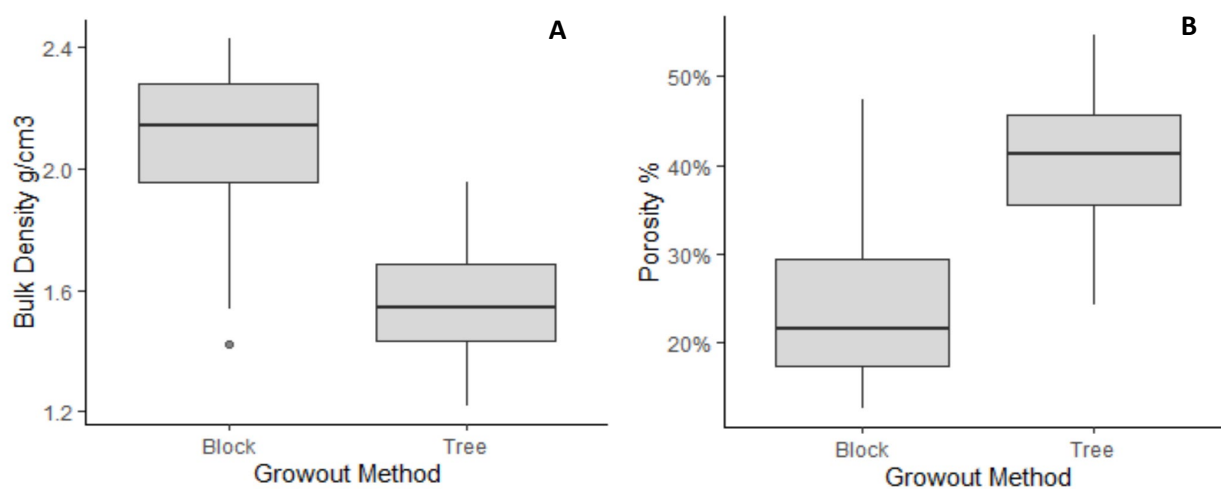


Fig. 8 Nursery-reared *A. cervicornis* exhibit different skeletal characteristics dependent on the grow out platform. (A) Corals grown on blocks are on average 35% more dense than corals grown on trees and (B) block-reared corals are on average 42% less porous than tree-reared corals.

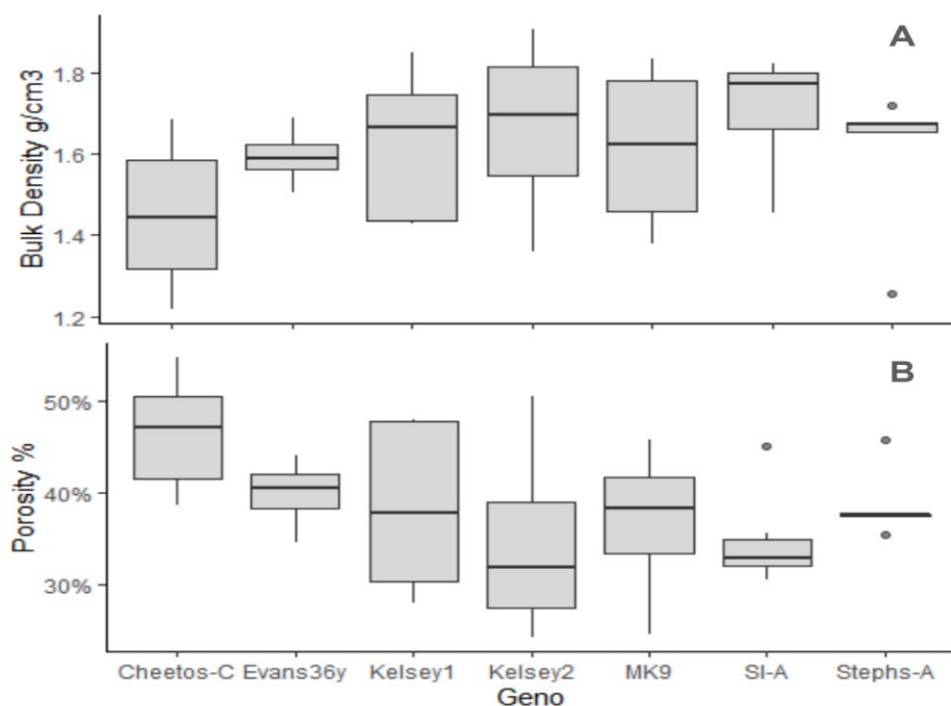


Fig. 9 Coral skeletal characteristics were not significantly influenced by the coral genotype for either (A) bulk density or (B) porosity.

Block-reared corals also had higher compressive strength (blocks = 30.53 ± 12.95 MPa, $n=24$; trees = 15.31 ± 7.53 , $n=10$; two-sample t test: $t=3.4598$, $p<0.01$; Fig. 10A) and increased flexural strength (blocks = 13.56 ± 5.09 MPa, $n=14$; trees = 7.89 ± 2.37 MPa, $n=9$; two-sample t test: $t=3.6006$, $p<0.01$; Fig. 10B) than mid-water tree-reared corals. Stress deformation plots are included in the appendix. The momentary decrease in applied load, seen as dips in the stress deformation curve, are explained by heterogeneous skeletal composition of coral skeletons. The maximum applied load is observed by physical fracturing of samples and is denoted as a peak on stress deformation curves. Compressive strength and bending strength were found to both be

positively correlated with diameter (Compressive: $r_p(32) = 0.766$, $p < 0.0001$; Flexural: $r_s(21) = 0.446$, $p < 0.05$; Fig. 11). Additionally, compressive and flexural strength were found to both be negatively correlated with porosity (Compressive: $r_p(32) = -0.711$, $p < 0.0001$; Flexural: $r_s(21) = -0.726$, $p < 0.001$; Fig. 12). However, both corals grown on trees and corals grown on blocks had mean ultimate bending strengths significantly greater than the bending stress either coral would be exposed to from wave energy on a reef under normal conditions (Fig. 13).

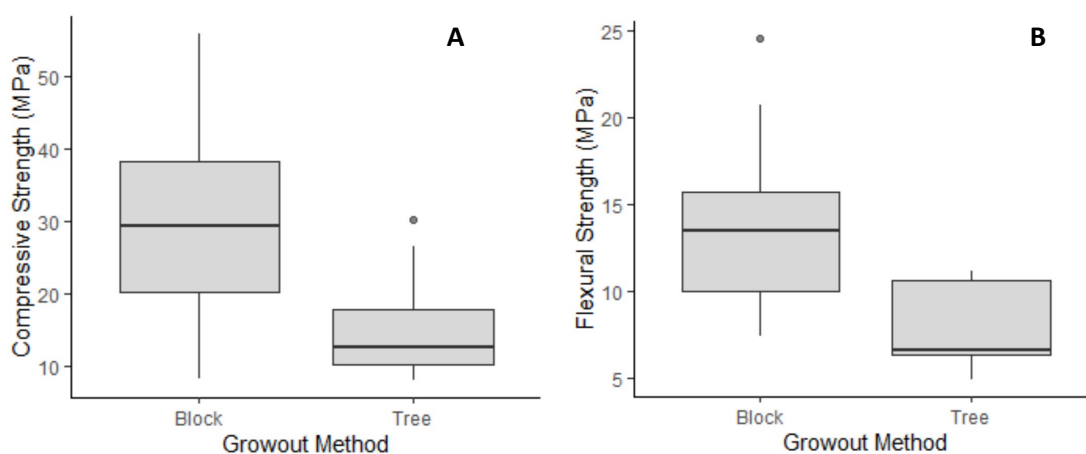


Fig. 10. The differences in nursery reared skeleton properties translated to increased strength in block reared corals **(A)** Block-reared corals had 99% greater compressive strength and **(B)** block reared corals had 72% greater flexural strength than tree-reared corals.

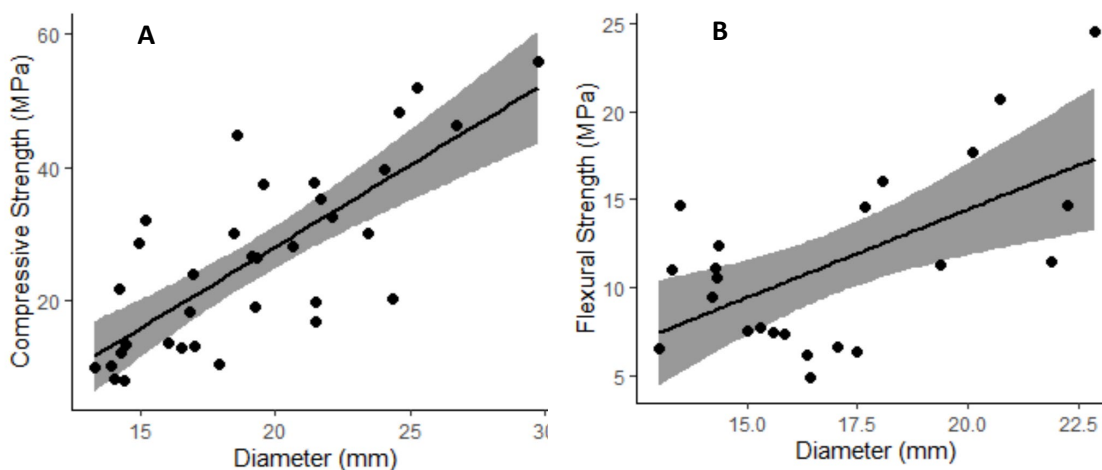


Fig. 11 Diameter is positively correlated with both (A) compressive strength, $r=0.77$, and (B) flexural strength, $r=0.45$. 95% conf interval denoted by grey boundaries.

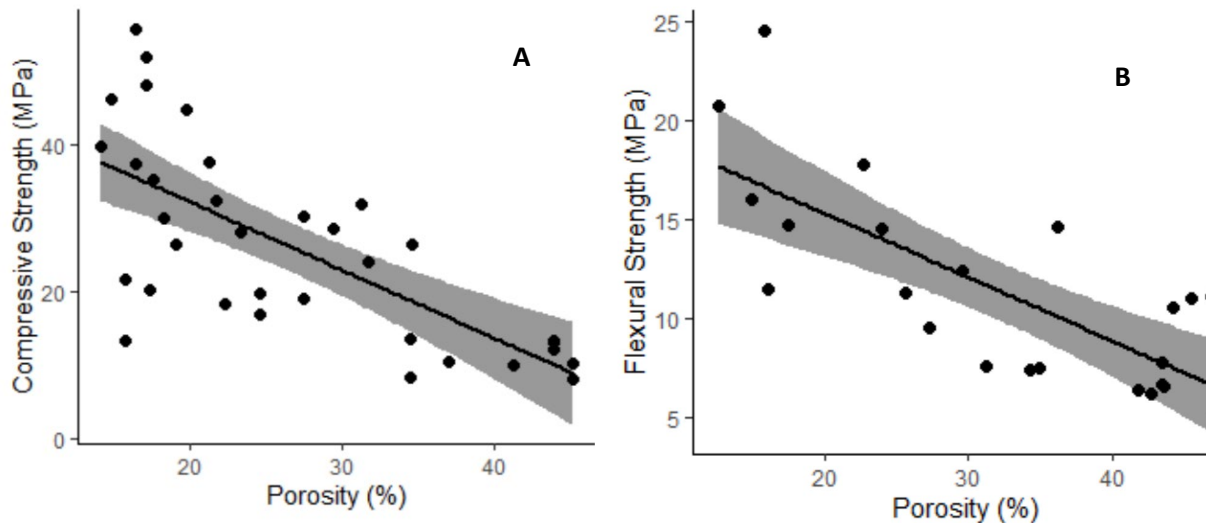


Fig. 12 Porosity is negatively correlated with both (A) compressive strength, $r=-0.71$, and (B) flexural strength, $r=-0.73$. 95% conf interval denoted by grey boundaries.

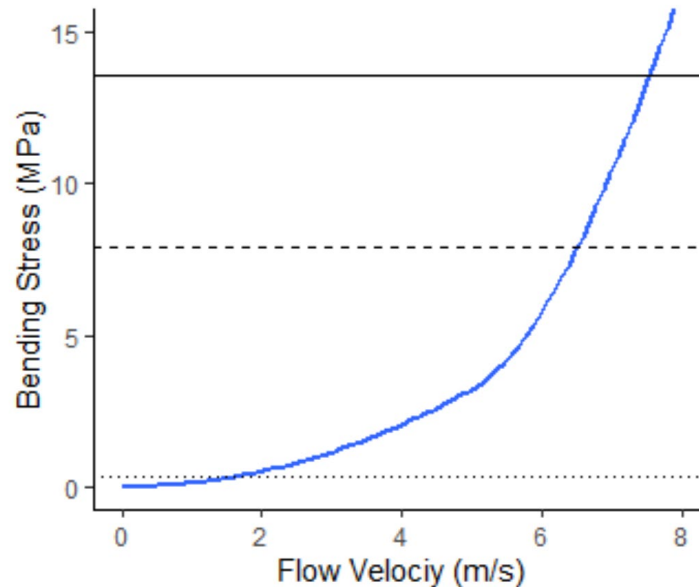


Fig. 13 Bending stress generated from wave flow Critical velocities required to create bending stress for tree-reared corals (dashed line) and block-reared corals (solid line) are significantly greater than that which corals would experience under normal (1 m/s) and tropical storm (5 m/s) conditions. Bending strength of the hard bottom substrate (dotted line) in the Great Barrier Reef is markedly less than that of either block or tree grown corals and the colony is likely to fragment at this interface before fragmenting at a branch within the colony (Madin 2005).

4.0 Discussion

Mechanical analysis of nursery-reared *A. cervicornis* suggest that corals grown on block structures are more resistant to wave loading than corals grown on floating tree structures. This increase in mechanical strength results from the increased average diameter and increased density of block-reared corals. Thus, corals grown on blocks may fragment less often under hydrodynamic stress. Wave action plays a key role in fracturing and dislodging coral colonies, particularly during severe hydrodynamic disturbances such as tropical storms (Lirman et al. 2001, Madin & Connolly 2006). Fragmentation is *A. cervicornis* most prolific form of reproduction; most colonies break from their bases and become reattached to the substrate, rapidly healing lesions and expanding upon the biomass of the parent colony (Tunncliffe 1981). However, there is a distinct balance between fragmentation as a reproductive strategy and detrimental fragmentation that diminishes coral cover and architectural complexity of reefs (Wulff 1995, Lirman et al. 2001, Boller et al. 2002).

Mechanical weakening during the growth phase in restoration nurseries and increased porosity from ocean acidification (OA) experiments may have a similar effect on coral colony persistence (Kuffner et al. 2017). Enochs et al. (2014) concluded that the increase in porosity and loss of structural integrity of corals exposed to OA conditions may further increase fragmentation and reduce the size of fragments which may have a detrimental impact on the reproductive success of *A. cervicornis* as fragments have a size-dependent survivorship, with larger size fragments experiencing lower mortality rates (Highsmith et al. 1980, Lirman 2000). Similarly, corals propagated on trees, which have increased porosity compared to block-reared corals (Fig. 7B), may have decreased asexual reproductive success.

Previous research by Kuffner et al. (2017) underscored the plastic skeletal traits that depended on grow-out method and the genetically influenced calcification of *A. cervicornis*. The results of the present study show that porosity and bulk density are environmentally plastic traits and are not significantly different across the seven genotypes tested (Fig. 7, Fig. 8). However, testing of additional genotypes should be explored for a more robust investigation of genotypic influence on skeletal density, porosity, and mechanical strength, but this influence, if present, is expected to be negligible compared to the strong influence of nursery grow-out platform. This is advantageous to restoration practitioners as they do not need to investigate nursery stock for specific genotypes. Rather, practitioners need only to implement block structures in their nursery to increase mechanical strength in coral stock.

Further, the corals grown on blocks in this study were significantly denser than corals grown on trees at two separate nursery locations. Previous studies investigating nursery structure influence on skeletal characteristics separately found significant influence of growth structure on skeletal density within the same nursery (Kuffner et al. 2017). Thus, the density of the corals, and therefore the mechanical strength, are more strongly influenced by the growth platform and are unlikely to be an artifact of the nursery location.

Despite the increase in mechanical strength of block-reared corals, coral skeleton's mechanical properties are not the limiting factor in determining coral colony's resistance to wave flow. Rather, the mechanical integrity of a colony is limited by the colony-substrate interface (Madin 2005). For instance, the strength of the hardbottom substrate in the Great Barrier Reef was considerably weaker and more variable than that of coral skeleton (Madin 2005). The surface substrate layer is an incredibly heterogeneous and porous mixture of coral rubble and crustose coralline algae cemented by secondary calcifiers (Rasser and Riegel 2002). *A.*

cervicornis grown on blocks and trees both have bending strengths greater than that of hard bottom substrate, and this interface is more likely to lead to colony dislodgement since the colony-substrate interface may be mechanically weaker than either the hard bottom substrate or the coral skeleton as often seen in Interfacial Transition Zones (ITZ) of cementitious materials (Prokopski & Halbiniak 2000). The shape of staghorn coral colonies has a high length to diameter ratio creating a high bending moment which places the drag forces at the base of the colony-substrate interface (Tunnicliffe 1981, Baldock 2014). This is distinct from that of massive colonies and congenics which have adapted growth morphologies and growth direction to experience compressive forces instead of drag forces or which have a wider diameter at the base of the colony to withstand the high bending moment (Schumacher & Plewka 1981, Madin 2005). Therefore, colonies with massive morphologies will not fragment as often as *A. cervicornis* despite being attached to the same hard bottom substrate (Fig. 14).

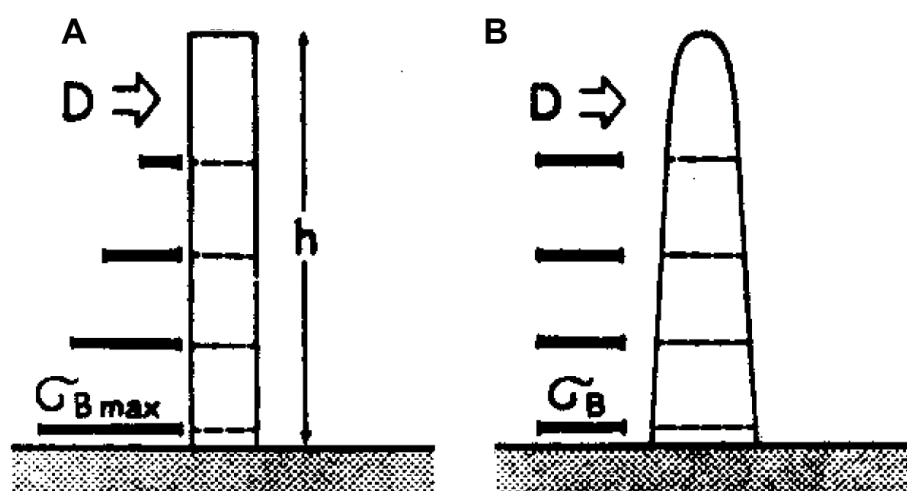


Fig 14 Comparison of stem-geometry in (A) *A. cervicornis* and (B) *A. palmata*. The high length to diameter ratio of *A. cervicornis* creates a high bending moment in the colony, while the tapered diameter along the span of *A. palmata* opposes the drag force experienced by the colony. Therefore, *A. cervicornis* will experience maximum bending stress (σ_B) at its base and *A. palmata* will distribute stress throughout the colony, reducing the stress at the colony-substrate interface and decreasing chances of whole-colony fragmentation. Reproduced from Schumacher and Plewka (1981)

The mechanical strength of branching corals, however, limits hydrodynamic pruning of branches within the colony which may be advantageous as survival of fragments might be size dependent (Highsmith et al. 1980, Madin 2005, Lirman et al. 2000). While the increased mechanical strength and increased average diameter of block-reared corals may better support a complex ramose structure, fragmentation of branches is unlikely to occur before whole-colony dislodgement and any increase in mechanical strength may not be realized (Schuhmacher & Plewka 1981, Madin 2005). This model is supported by field-based observations which saw most colonies fragmenting and re-adhering to the substrate at its base (Tuncliffe 1981). On a fore reef, normal daily maximum wave velocities are expected to be less than 1 m/s, while tropical cyclones may generate wave velocities of approximately 5 m/s (Madin 2004). Water motion alone is unlikely to break coral branches (Fig. 13), but branches may still break from waterborne projectiles such as unattached fragments or debris (Madin 2005). Greater structural strength may allow block-reared corals to better resist branch fragmentation than tree-reared corals, but this form of fragmentation is unlikely to occur before whole-colony dislodgement which is largely dependent on the hardbottom substrate of the colonies (Madin 2005). The benefit, therefore, of using block platforms in coral nurseries to decrease colony fragmentation is marginal, if at all present. But there may be benefits from decreased branch fragmentation including increased rugosity from maintaining colony size or increased energetic reserves from not having to expend energy resources on lesion healing of fragmented branches (Lirman 2000). Outplanting using concrete with select aggregates may decrease whole-colony fragmentation by increasing the ITZ strength of the colony and substrate (Kim & Robertson 1998, Duan et al. 2013). Additional mechanical testing is recommended to determine the structural strength of the colony-substrate interface and of common outplanting mediums to select candidate methodologies and aggregates

for outplanting corals in high energy environments. Additionally, development of novel techniques that limit boring in outplants, which has been shown to markedly decrease structural integrity (Scott and Risk 1988), may also increase outplant persistence more so than using block structures.

5.0 Conclusion

In agreement with previous studies investigating the plastic morphology of nursery-reared staghorn corals, corals grown on blocks are significantly denser and less porous than corals grown on trees. These growth characteristics increase the mechanical strength of coral skeletons and may decrease fragmentation of branches in outplanted coral stock. This may be particularly advantageous when restoring reefs in high wave energy environments. However, the persistence of outplanted corals, as concluded in previous biomechanical analyses of coral reefs, may not be influenced by skeletal strength as much as it is by the colony-substrate interface, where the hardbottom substrate is an order of magnitude less strong than the coral skeleton for either block or tree grown corals. Therefore, we recommend that restoration practitioners focus on mitigating boring species and implement outplanting methodologies that increases the bond strength of the coral and hardbottom substrate to decrease whole-colony fragmentation in high energy environments.

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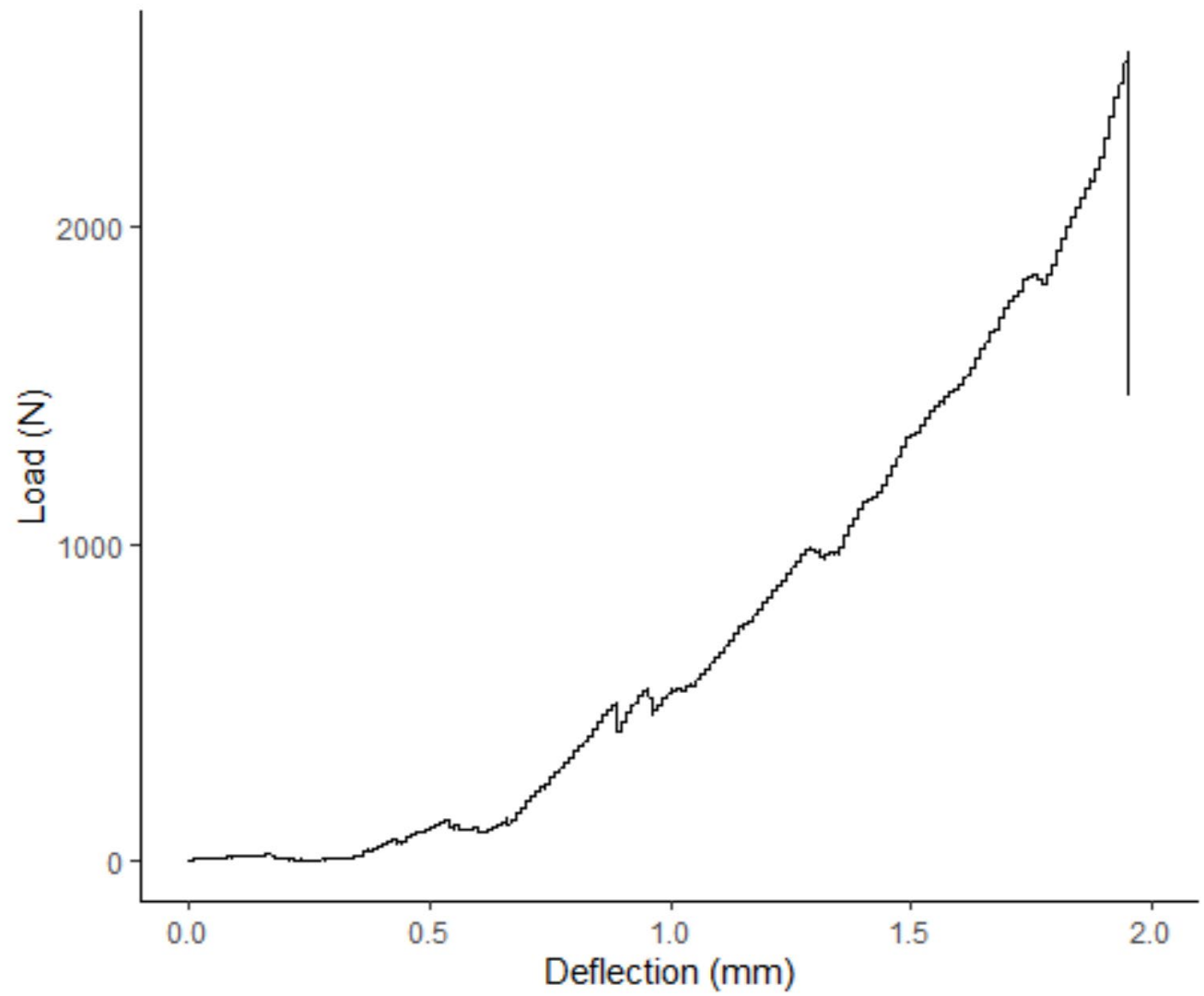
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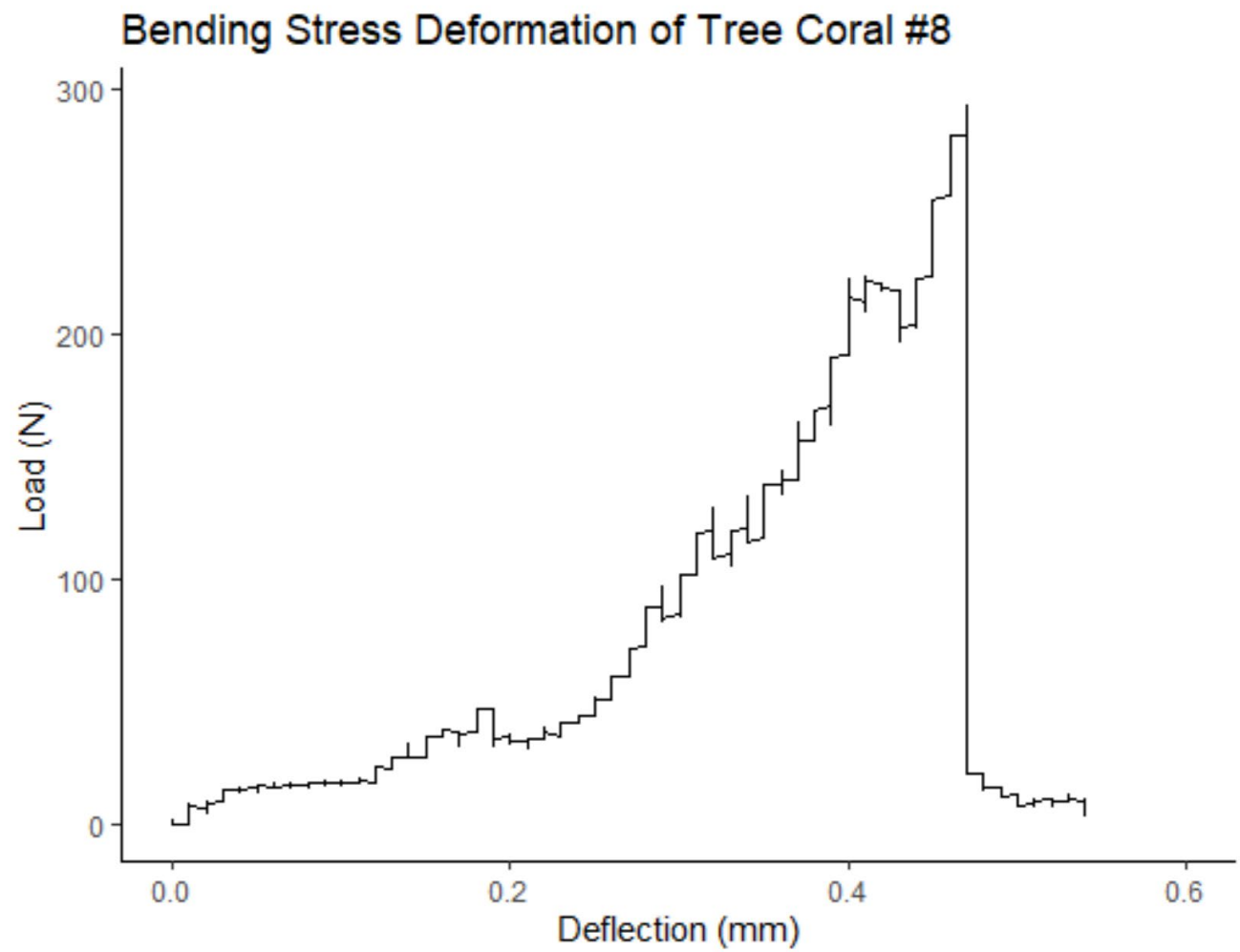
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Appendix

Bending Stress Deformation of Block Coral #7





Compressive Stress Deformation of Block Coral #42

