QUANTIFYING THE EFFECTS OF COLONY SIZE, MORPHOLOGY, AND BLEACHING ON GROWTH RATES OF THE CORAL *MONTIPORA CAPITATA* USING 3D STRUCTURE-FROM-MOTION PHOTOGRAMMETRY

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ABSTRACT

Coral growth plays a vital role in forming the structural complexity that supports reef biodiversity, but can vary widely across species and locations, with Hawaiian corals reported to be among the slowest growing. Here we follow 103 individual colonies of the Hawaiian scleractinian coral *Montipora capitata* over 21 months to quantify growth using 3D models created using Structure-from-Motion (SfM) photogrammetry. Colony size, rugosity, and bleaching occurrence were significant predictors of coral growth rate, which increased colony size by an average of 180% (planar area) to 210% (3D surface area). Both measures of area were significantly correlated (r=0.98), highlighting the utility of either measure, even in a species with highly plastic growth morphology like *M. capitata*. Total growth was positively correlated with colony size such that larger colonies grew more than smaller ones, but proportional growth was highest (up to ~3% / day) in small colonies. Rugosity was negatively correlated with growth rate, as colonies with plating morphologies grew faster than branching morphologies. The relationship between rugosity and size is complicated, however, because rugosity increased significantly throughout the study with smaller colonies showing the greatest increase in rugosity through time. Corals that experienced bleaching during the 2019 heat wave (35 of 103) showed significantly lower growth (1.67 fold) than colonies that did not bleach, despite 100% recovery of bleached colonies. This study highlights some of the complexity in estimating and comparing coral growth rates and documents a long-term impact of non-lethal bleaching on subsequent coral growth rate.

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CHAPTER 1

A Review of Factors Affecting Coral Growth and Methods used to Assess Coral Growth Rates

Introduction

Coral reefs comprise only 0.2% of the ocean's area, yet they are home to nearly one third of all marine life (Knowlton et al. 2010). The extraordinary biodiversity found in coral reef ecosystems has earned them the title "rainforests of the sea," with estimates of coral reef species richness ranging from 490,000 (Bouchet 2006) to 9,477,000 species (Reaka-Kudla 1997). Of these reef species, there are less than 1,000 species of scleractinian corals that form the foundation of coral reefs. Scleractinian corals build calcium carbonate skeletons that provide three-dimensional (3D) habitat structure that supports the extensive biodiversity of fish, invertebrates, and other animals on coral reefs (Graham & Nash 2013, Burns et al. 2019, Urbina-Barreto et al. 2021). However, global increases in sea surface temperature (SST) and ocean acidification (OA) pose significant threats to coral reef ecosystems by causing increases in the frequency of coral bleaching and decreases in coral growth rates (Cantin et al. 2010, Guo et al. 2020, Crabbe 2008). Identifying and quantifying factors that affect coral growth can inform coral conservation and restoration efforts that work to protect coral reefs from the stressors of climate change.

Coral growth is influenced by a diversity of factors causing variation among species (Pratchett et al. 2015, Dullo 2005, Minton 2013, Morgan & Kench 2012, Huston 1985, Rodgers et al. 2003, Lough & Barnes 2000), within a single species across the species distribution (Pratchett et al. 2015, Minton 2013, Grigg 1998, Grigg 1982), and within a single coral across its lifetime (Muko et al. 2000, Million et al. 2022, Elliott et al. 2016, Todd 2008). Differences in growth rates occur on multiple spatial scales, even when controlling for taxonomy and morphotype (Grigg 1982, Browne 2012, Pratchett et al. 2015, Minton 2013). At large scales, for example, growth rates within multiple coral genuses decline significantly with increasing latitude

(Grigg 1982, Lough & Barnes 2000, Nozawa et al. 2021), and growth rates of *Pocillopora damicornis* corals are up to eight times faster in the Philippines than in Hawaiʻi (reviewed in Minton 2013). At a small scale at a single site on the Great Barrier Reef, Browne (2012) documented almost two-fold differences in intraspecific growth rates among coral colonies living in different habitats on the reef for three different coral genuses (*Acropora, Montipora,* and *Turbinaria*). Numerous environmental factors drive such differences in coral growth rate and growth strategy (Pratchett et al. 2015), including nutrient levels (Atkinson et al. 1995, Savage 2019), wave exposure (Grigg 1998, Smith et al. 2007, Lough & Barnes 2000), light level (Hubbard & Scaturo 1985, Forsman et al. 2011, Muko et al. 2000), temperature (Anderson et al. 2017, Cantin et al. 2010, Lough & Barnes 2000), pH (Guo et al. 2020), and even hormones that pollute coastal waters, such as estrogens (Tarrant et al. 2004).

To isolate how specific properties of coral biology, including colony size, morphology, and susceptibility to bleaching, influence colony growth rate, this review chapter focuses on the impact of these three factors (size, morphology, and bleaching) on coral growth rates across a diversity of species and on variations in growth rates within species. We also evaluate the various techniques employed to measure coral growth and establish a case for using 3D Structure-from-Motion photogrammetry as the best approach to address the hypotheses of this study and build a database for future coral growth studies. We close with a summary of coral growth estimates in the Hawaiian Archipelago and provide additional background on Kāneʻohe Bay and *Montipora capitata*, the site and coral species for this study.

Variation in Coral Growth Rate with Colony Size

Scleractinian corals are colonial cnidarians that, in theory, can grow indefinitely (i.e. indeterminately) by adding modules to their colony through asexual reproduction (Kim & Lasker 1998, Pratchett et al. 2015). However, their growth is limited by both intrinsic factors, such as structural constraints and energy allocation, and extrinsic factors, such as partial mortality due to herbivory and skeletal breakage (Kim & Lasker 1998, Dornelas et al. 2017). Generally, larger corals grow more in total size than smaller corals, but smaller corals grow proportionally faster than larger corals of the same species (Lirman et al. 2014, Bak 1976, Yap 1998, Hughes & Connell 1987, Pratchett et al. 2015). This decrease in proportional growth rate with increasing colony size is expected due to mechanistic constraints on growth. In order to maintain constant proportional growth rates, coral colonies would need to calcify new skeleton at an increasing rate as colony size increases (Hughes & Connell 1987), but calcification rates do not significantly differ between small and large colonies when scaled per unit of projected surface area to account for living calcifying tissue (Bak 1976). This suggests that net growth rate decreases with increasing colony size following the laws of allometric scaling (Dornelas et al. 2017, Million et al. 2021, Edmunds & Putnam 2020, Lirman et al. 2014). Faster growth in smaller colonies may be a mechanism for corals to gain a competitive advantage for reef space or to avoid higher mortality rates associated with smaller colony size (Rodgers et al. 2003, Forsman et al. 2015, Edmunds 2021), while reduced growth in larger colonies could be due to a decrease in energy allocation to growth in favor of an increase in energy for reproduction (Richmond 1987). This may not be the case for all corals, though, as some increase their growth rates at the onset of reproduction (Chorensky & Peters 1987).

An alternative theory is that coral growth rates scale isometrically, exhibiting constant growth across colony size (Madin et al. 2020, Carlot et al. 2022). However, the distinction between isometric and allometric growth depends on how coral growth is quantified (Madin et al. 2020, Carlot et al. 2022). For example, Madin et al. (2020) found that corals exhibit allometric net growth (growth accounting for partial mortality), but non-allometric total growth (growth in the absence of partial mortality), and Carlot et al. (2022) found differences in scaling among physiological processes contributing to growth; calcification rates scale allometrically, while photosynthetic and respiratory rates scale isometrically. For predicting growth rate over time, Edmunds & Putnam (2020) suggest that scaling coral growth by biomass is more accurate than scaling by area. In a study distinguishing colony size from age, Sandin et al. (2020) show that growth is independent of initial colony size and instead a function of colony age. Altogether, these studies underscore the complexity of coral growth that emphasizes the need for additional studies quantifying multiple measures of coral growth to more fully understand how coral growth rates vary across colony size.

Morphological Variation in Coral Growth Rate

While substantial evidence supports the control of environmental factors on coral morphology (Buddemeier & Kinzie 1976, Chappell 1980, Pratchett et al. 2015, Smith et al. 2007, Lough & Barnes 2000, Kahng et al. 2020, Kaandorp et al. 1996, Rodgers et al. 2003, Muko et al. 2000), fewer studies have investigated specific differences in growth rate with growth morphology. Generally, however, branching corals in the families Acroporidae and Pocilloporidae exhibit higher growth rates than massive corals in the family Poritidae (Pratchett et al. 2015, Dullo 2005). Differences in growth rates among morphologies are substantial. Across taxonomic groups, branching and digitate coral species exhibit up to 25 times faster extension rates than massive and encrusting species (Huston 1985, Morgan & Kench 2012). Pratchett et al. (2015) also provide evidence that branching corals grow faster than massive corals and draw additional comparisons between more specific morphologies. Among coral species with branching morphologies, arborescent (open branching) and tabular corals have faster extension rates than corymbose (irregular branching) and digitate corals (Pratchett et al. 2015). Corymbose and digitate corals have stronger skeletal bases of attachment to the substrate than arborescent and tabular corals do (Wallace 1999, Pratchett et al. 2015), so they may allocate more energy to the growth of these structural bases than to the extension of their branching skeletons.

In addition to differences in growth across species, certain species of corals exhibit phenotypic plasticity that allows them to grow in different morphologies when subjected to different environmental parameters (Muko et al. 2000, Todd 2008, Million et al. 2022) or when competing with other species (Elliott et al. 2016). For example, colonies of *Porites sillimaniani* grow in branching morphologies in high light conditions and in plating morphologies in low light conditions (Muko et al. 2000). Off the island of Mauritius in the Indian Ocean, colonies of *Montipora aequituberculata* commonly grow in foliose morphologies, but were observed growing in encrusting morphologies when competing with the sponge *Terpios hoshinota* (Elliott et al. 2016). These findings are consistent with the idea that morphological plasticity is adaptive in corals; corals that exhibit greater morphological changes over time experience reduced mortality rates and increased growth rates (Million et al. 2022). Therefore, understanding the variation in growth rates across morphologies within the same species is important for predicting how coral communities will change over time.

Impacts of Coral Bleaching on Growth Rate

As climate change continues to increase the frequency and severity of coral bleaching events (Crabbe 2008, Cantin et al. 2010), an increasing number of studies have investigated the effects of bleaching on coral growth. Negative effects of bleaching on coral growth rates have been documented in a variety of coral species and locations around the world (Goreau & Macfarlane 1990, Tudhope et al. 1993, Lough & Cantin 2014, Carilli et al. 2009, Carilli et al. 2010, Carilli et al. 2012, D'Olivo et al 2013, Gold & Palumbi 2018). Up to 45% slower skeletal extension rates have been documented in corals after bleaching, but reductions in growth may be lower in corals living at sites with higher thermal variability prior to bleaching (Carilli et al. 2012). Long-term trends indicate that even the growth of healthy colonies has declined by up to 30% in the past two decades due to rising SSTs (Cantin et al. 2010).

The effects of bleaching on growth rates vary among species, with some species experiencing no negative effects of bleaching on growth while others in the same location experiencing reduced rates of growth after bleaching (Baumann et al. 2019). Documented times for coral growth to return to pre-bleaching rates have ranged from 4 months (Baird & Marshall 2002) to 8 years (Carilli et al. 2009). Variation in recovery timelines may be species-dependent (Baird & Marshall 2002), and time to return to pre-bleaching growth rates may be longer for more severely bleached corals (Cantin & Lough 2014) and at sites with higher levels of anthropogenic stress (Carilli et al. 2009).

Coral growth in response to bleaching is colony-specific and varies both within and among species, possibly as a function of environment. Forsman et al. (2011) provide evidence of both intrinsic and extrinsic factors affecting coral bleaching and growth: *Montipora capitata* corals bleached and grew poorly in high light and low flow conditions, while *Porites compressa* corals did not bleach and grew fastest in the same conditions. Additionally, declines in coral skeletal extension after bleaching differed between colonies of *Sidersatrea siderea* and *Pseudodiploria strigosa* and were found only at some sites on the Belize Mesoamerican Barrier Reef System (primarily those characterized as nearshore with higher exposure to anthropogenic stressors; Baumann et al. 2019). Similarly, reductions in linear extension rates of *Porites* in the Gilbert Islands after a 2004 bleaching event were lower in corals at a site with high thermal variability than in corals at a site with lower thermal variability, suggesting that corals in more highly variable sites were more acclimatized to thermal stress (Carilli et al. 2012).

On a landscape scale, Loya et al. (2001) showed that coral species with massive and encrusting morphologies are bleaching "winners" that had higher tissue thickness and increased their percent cover and abundance on the reef after bleaching, while coral species with branching and plate-like morphologies are "losers" that had lower tissue thickness and a decreased percent cover and abundance after bleaching. "Winners" and "losers" also exist within species with variation in size-dependent bleaching and mortality on a colony-scale (Speare et al. 2022), but the exact relationship between colony size and thermal stress response is unclear. Some data indicate that smaller colonies are more susceptible to bleaching than larger colonies of the same species (Johnston et al. 2020), while others document disproportionate effects of bleaching (Shenkar et al. 2005) and thermal stress and mortality (Kopecky et al. 2023, Speare et al. 2022) on larger colonies. These differences between trends in bleaching susceptibility and mortality may be a result of interspecies variability, since these studies all measured different species.

Within coral species, complex tradeoffs between bleaching resistance and growth rate confound the relationship between bleaching and growth (Goreau & Macfarlane 1990, Cornwell et al. 2021, Walker et al. 2022, Gold & Palumbi 2018, Forsman et al. 2011). In *Acropora* *hyacinthus,* for example, Walker et al. (2022) found that corals with moderate heat resistance grew more than conspecifics with both high and low heat resistance, but Gold & Palumbi (2018) documented two times faster growth rates in corals with low heat tolerance compared to those with high heat tolerance of the same species. However, corals with high heat resistance suffered less mortality than those with moderate and low heat resistance, suggesting that there are tradeoffs between bleaching resistance and growth rate when survival is at stake (Walker et al. 2022).

Methodological Considerations for Assessing Coral Growth Rates

One of the factors confounding growth rate measurements in corals is the variation in the approaches used to quantify growth, which are often not comparable across studies. Studies quantifying coral growth rates have employed a variety of measurement techniques that vary in accuracy, precision, practicality, and application to specific research objectives. As reviewed by Pratchett et al. (2015), these include: (1) direct measurements of skeletal linear extension, either by tagging branches to be repeatedly measured with rulers or calipers (Shinn 1966), or by staining corals, such as with alizarin dye, to measure growth from the time of staining (Holcomb et al. 2013); (2) indirect measures of skeletal growth, such as the buoyant weight technique (Jokiel et al. 1978) and the alkalinity anomaly technique (Chisholm & Gattuso 1991); (3) measurements of coral surface area, such as those obtained from dipping corals in wax (Stimson & Kinzie 1991) or covering them in tinfoil (Marsh 1970); (4) retrospective measures of coral growth from skeletal core growth bands (Knutson et al. 1972); and (5) measurements of changes in colony dimensions using digital imagery (Ferrari et al. 2017). The application of each method depends on experimental design, the types of samples available, the questions being addressed, and the goals and timescale of the study.

Coral growth measurement methods demonstrate varying degrees of precision and accuracy due to differences in their application and output. For example, manual measurements of coral skeletal core growth bands are associated with a greater degree of human error than more objective methods such as the buoyant weight technique (Pratchett et al. 2015). Different methods are also more suitable for specific coral morphologies, such as linear extension measurements for branching corals, coral core growth band measurements for massive colonies, and measurements of change in planar area from digital images for encrusting corals (reviewed in Pratchett et al. 2015). The degree of error in growth rate estimates for different coral morphologies may depend on both the technique used to measure growth (Figueira et al. 2015) and the mechanism of growth (Lange & Perry 2020). The rugosities of tabular or plate-like morphologies, for example, are the most underestimated from 3D photogrammetry measurements (Figueira et al. 2015). Coral growth mechanisms also differ among morphologies, such that growth occurs in different dimensions or at different parts of a colony (Lange & Perry 2020). Branching and digitate corals, for example, grow mainly from branch tips, so their growth is best measured in linear extension. Massive and encrusting corals, on the other hand, grow in all directions, so their growth is best measured in radial extension. (Lange & Perry 2020).

Due to these differences in growth strategies, the most common method of measuring coral growth as linear skeletal extension may underestimate the extent of growth for many types of massive and encrusting colonies. For example, Morgan and Kench (2012) found that branching and digitate coral species exhibit up to 25 times faster extension rates than massive and encrusting species. However, the techniques Morgan and Kench (2012) used to measure skeletal extension included alizarin staining and direct caliper measurements, which may report higher rates of skeletal extension for corals that grow by extending their branching skeletons than for corals that grow by encrusting on a surface or adding mass to their mounding morphologies (Pratchett et al. 2015). Both alizarin staining and caliper measurements record skeletal growth in only one dimension, so they more accurately report the primarily one-dimensional, vertical growth of branching corals than the multi-dimensional growth of massive or encrusting corals (Pratchett et al. 2015). A more comprehensive method of measuring coral growth in all dimensions is necessary to provide more accurate, comparable data on growth rates for all types of coral morphologies.

Structure-from-Motion Photogrammetry

Standardized comparisons among coral growth rate studies are vital for understanding how coral growth differs across time and in different parts of the world (Edmunds et al. 2019). However, the disparities in methods used to estimate coral growth have produced large variation in coral growth rate estimates (reviewed in Minton 2013, Pratchett et al. 2015) and make it difficult to compare past work to present work, emphasizing the need to adopt a standardized, universal method for measuring coral growth rates. Digital imagery quantifications are some of the most recently developed and comprehensive methods of measuring coral growth in three dimensions, allowing for more accurate, comparable data on growth rates for all types of coral morphologies. Structure-from-Motion (SfM) photogrammetry is one use of digital imagery that offers a standardized, non-invasive, efficient, and relatively inexpensive way to document coral cover by capturing and processing overlapping photographs of a reef (Burns et al. 2015, Suka et al. 2019, Roach et al. 2021). These photographs can be captured underwater by a snorkeler or scuba diver, or above the water via drone. From SfM data, three-dimensional (3D) models of coral reefs can be created using a digital image processing program. SfM allows for detailed and accurate characterization of individual coral colonies by providing both two-dimensional (2D) and 3D metrics of coral size and morphology in one comprehensive procedure.

Estimates of coral colony linear extension (Million et al. 2021), area (Kikuzawa et al. 2018), surface area (SA; Conley & Hollander 2021), and volume (Curtis et al. 2023) from 3D SfM photogrammetry are comparable to (Conley & Hollander 2021) or more accurate than (Curtis et al. 2023) manual *in-situ* measurements and calculations from linear measurements (Kikuzawa et al. 2018). SfM photogrammetry can also quantify metrics that relate to ecological characteristics of coral reefs, such as the structural complexity of coral colonies (Burns et al. 2015, Young et al. 2017, Fukunaga & Burns 2020, Leon et al. 2015) that predict patterns of reef biodiversity (Curtis et al. 2023).

Some limitations have been identified for 3D SfM approaches. For example, measurements of planar area and SA from 3D photogrammetry models may not fully capture vertical growth in morphologically complex coral colonies, leading to underestimates of growth (Lange & Perry 2020, Curtis et al. 2023). Specifically, measurements from photogrammetry underestimate coral volume compactness and surface complexity compared to 3D light scanning techniques (Guendulain-García et al. 2022). Despite these limitations, measuring coral growth using 3D photogrammetry presents an accessible method to improve the extent of information obtained from measuring coral growth and to standardize coral growth rate data for more accurate comparisons across studies (Couch et al. 2021, Guendulain-García et al. 2022, Conley

& Hollander 2021, Curtis et al. 2023). The digital accessibility of 3D SfM models enables these comparisons and allows new information to be re-analyzed by continuously contributing updated models to a permanent digital record.

Hawaiian Coral Growth

Coral reefs in the Hawaiian Archipelago exist in isolation in the middle of the Pacific Ocean and have been the subjects of a variety of studies that have directly measured shallow-water scleractinian coral growth (Edmondson 1929, Maragos 1972, Buddemeier & Kinzie 1976, Jokiel & Coles 1977, Cox 1986, Atkinson et al. 1995, Grigg 1998, Grottoli 1999). Hawaiian coral growth rates range from negligible annual growth in multiple species (reviewed in Minton 2013) to growth as high as 4.76 cm per year in *Pocillopora eydouxi* (Kolinski 2007). Relative to other reefs in the Indo-Pacific, Hawaiian coral reefs generally lack an abundance of faster-growing genuses such as *Acropora* that contribute to the high growth rates observed at other sites in the Indo-Pacific (reviewed in Minton 2013), with estimates of up to 33.3 cm of growth per year in *Acropora valenciennesi* in Indonesia (Crabbe and Smith 2005). However, Hawaiian reefs are abundantly populated by *Montipora* corals, which are in the *Acroporidae* family and exhibit the second highest growth rate of Hawaiian corals after *Pocillopora eydouxi* (Grottoli 1999, Kolinski 2007, reviewed in Minton 2013).

Although reports of Hawaiian coral growth rates span a diversity of species and sites across the Archipelago (reviewed in Minton 2013), some species and sites are understudied compared to others. For example, *Porites lutea* growth rates in Hawaiʻi are represented by a single published estimate, while *Porites lobata* growth rates across the Archipelago have been estimated by seven different published studies (reviewed in Minton 2013). An increase in targeted studies focusing on specific species in distinct locations will provide a more comprehensive collection of updated growth reports to monitor Hawaiian coral growth rates over time. Kāneʻohe Bay on Oʻahu is one of the most studied coral reef habitats in the world (Bahr et al. 2015, Hunter & Evans 1995, reviewed in Minton 2013), and corals in the bay make excellent candidates for targeted growth rate studies: they are abundant, diverse, have overcome past bleaching events and other stressors, and reside in an ecosystem that has been studied for decades (Bahr et al. 2015, Hunter & Evans 1995, Bathen 1968, Jokiel 1991).

Montipora capitata is among the most abundant (Edmondson 1929, Maragos 1972, Jokiel 1991) and fastest-growing coral species in Kāneʻohe Bay (Minton 2013). The highest reported growth rate for the species was recorded by Grottoli (1999), who reported a maximum linear skeletal extension (MLSE) equivalent to 4.27 cm of growth per year. Additional growth rate estimates for *M. capitata* in Kāneʻohe Bay include 1.65 - 2.92 cm of growth in linear extension per year (Cox 1986), 2.43 cm of growth in linear extension per year (Rodgers et al. 2003), 3.25 cm of inter-crest radial growth per year (Stimson 1996), and 3.60 cm of growth in maximum diameter per year (Holthus et al. 1986). Despite measuring growth rates for the same species in the same general location, the difference between the highest and lowest of these recorded values is over 2.5 cm per year, which is greater than some of the growth rate estimates themselves. This variation in growth could be due to temporal changes in coral growth rates, small-scale spatial variation between sites in Kāneʻohe Bay, or differences in the measurement methods used to estimate growth. Using SfM photogrammetry to measure the growth rates of *M. capitata* corals ranging in size and morphology and growing in a relatively stable environment in Kāneʻohe Bay will help to identify factors contributing to differences among coral colony growth in morphologically diverse coral species.

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CHAPTER 2

Quantifying the Effects of Colony Size, Morphology, and Bleaching on Growth Rates of the Coral *Montipora capitata* using 3D Structure-from-Motion Photogrammetry

Introduction

Coral reefs are among the most biodiverse ecosystems in the world, hosting roughly one third of all marine species (Knowlton et al. 2010, Fisher et al. 2015). Scleractinian reef-building corals are foundation species in these ecosystems, providing the three-dimensional (3D) structure that supports this extraordinary biodiversity (Graham & Nash 2013, Burns et al. 2019, Urbina-Barreto et al. 2021). However, global increases in sea surface temperature (SST) pose significant threats to coral reef ecosystems by increasing the frequency of coral bleaching (Crabbe 2008, Cantin et al. 2010, Guo et al. 2020). Bleaching is a thermal stress response that can cause coral growth rate to decrease (Gold and Palumbi 2018, Walker et al. 2023) due to the loss of the symbiotic zooxanthellate algae that typically provide corals with most of their energy by photosynthesizing within living coral tissue (Douglas 2003, Blackstone & Golladay 2018). Amidst ongoing threats of bleaching and other stressors, characterizing how reef structure is created and maintained by the growth of individual coral colonies is essential to understanding the role and resiliency of corals as ecosystem engineers.

In the Indo-Pacific, annual coral growth rates vary widely across species and locations (Highsmith 1979, Harriott 1999, Grottoli 1999, Morgan & Kench 2012, Anderson et al. 2017), with estimates ranging from 0.1 cm per year in *Porites lobata* (Clark & Edwards 1995) to 33.3 cm per year in *Acropora valenciennesi* (Crabbe and Smith 2005). Coral growth rate is strongly correlated with morphology, with branching and digitate coral species exhibiting up to 25 times faster extension rates than massive and encrusting species (Huston 1985, Morgan & Kench 2012). Even among coral species with branching morphologies, arborescent (open branching) and tabular corals have faster extension rates than corymbose (irregular branching) and digitate corals (Pratchett et al. 2015), possibly because corymbose and digitate corals allocate more energy to growing stronger skeletal bases of attachment to the substrate (Wallace 1999, Pratchett et al. 2015) while arborescent and tabular corals allocate more energy to skeletal branch extension.

In some cases, differences in growth rate are correlated with morphological changes caused by environmental differences (Buddemeier & Kinzie 1976, Chappell 1980, Pratchett et al. 2015, Smith et al. 2007, Todd 2008, Elliott et al. 2016, Lough & Barnes 2000, Kahng et al. 2020, Kaandorp et al. 1996, Rodgers et al. 2003), such as branching colony growth in high light conditions and plating colony growth in low light conditions (Muko et al. 2000). In other cases, however, the dynamic relationship between environment, morphology, and growth rate is more difficult to discern. *Platygyra daedalea* corals, for example, have been observed growing in up to seven different morphologies in the same environment (Miller 1994), and 23% of individually marked *Pocillopora* corals in the Eastern Tropical Pacific changed morphology over the course of 44 months sufficiently enough to be identified as different species (Paz-Garcia et al. 2015). In Hawaiʻi, *Montipora capitata* corals grow along a spectrum of morphologies, ranging from branching to plating, with little to no observed correlation with environmental factors or resource availability (Forsman et al. 2010, Cunha et al. 2019). In this study, we explore the interactions between morphology and growth rate in *M. capitata* corals in Hawaiʻi.

Montipora capitata corals exhibit extraordinary phenotypic variability; colony morphology ranges between laminar, encrusting, plating, and branching forms, and colony color appears in shades of red, orange, brown, and yellow (Forsman et al. 2010, Cunha et al. 2019). The variation in *M. capitata* morphology does not appear to be driven by genotypic differences (Forsman et al. 2010, Cunha et al. 2019), but to our knowledge, the links between environment, morphological change, and growth in this species has not been explored. Here, we quantify growth rates of *M. capitata* coral colonies in a floating nursery at the Hawai‘i Institute of Marine Biology (HIMB) in Kāne‘ohe Bay, O‘ahu. Kāne‘ohe Bay is one of the most studied coral reef habitats in the world (Bahr et al. 2015, Hunter & Evans 1995, reviewed in Minton 2013), and *M. capitata* is one of the most abundant coral species in the bay (Edmondson 1929, Maragos 1972, Jokiel 1991). *Montipora capitata* coral colonies are also abundant in the HIMB coral nursery, where they grow in a relatively sheltered habitat along a spectrum of sizes and morphologies ranging from branching to plating forms, with some colonies exhibiting a combination of morphologies. A thermal stress event in 2019 had varying impacts on colonies in the nursery, as some colonies exhibited visible bleaching while others did not. We use this bleaching event and the abundance of phenotypically variable *M. capitata* colonies in the HIMB nursery as an opportunity to examine the dynamic interactions between coral growth rate and coral colony size, morphology, and bleaching occurrence.

Here, we quantify and compare *M. capitata* growth rates utilizing Structure-from-Motion (SfM) photogrammetry (Burns et al. 2015, Suka et al. 2019, Roach et al. 2021) and the computer programs Agisoft Metashape™ (Agisoft LLC, St. Petersburg, Russia) and TagLab (Pavoni et al. 2022) to create and analyze 3D models of 103 *M. capitata* coral colonies in the HIMB coral nursery over the course of 21 months. We classified each of the colonies as bleached or not bleached at the onset of the study in 2019 to assess whether the occurrence of bleaching affected subsequent growth rate. We include colonies across the range of *M. capitata* morphotypes, which we quantify as surface rugosity, to document the relationship between colony morphology and growth rate, and we include colonies across a spectrum of sizes to document the relationship between colony size and growth rate. The ability of the SfM method to capture coral colonies in

3D allows us to assess how colony bleaching, morphology, and size affect *M. capitata* growth over time, offering new insights into intraspecific variation in colony-scale growth rates.

Methods and Experimental Design

Study Site

We conducted this study in an *in-situ* floating coral nursery at the Hawaiʻi Institute of Marine Biology (HIMB) in Kāneʻohe Bay on the island of Oʻahu, Hawaiʻi (Fig. 1). The nursery consists of 15 floating PVC pipe racks separated by floating docks into six enclosed sections that cover an area of approximately 200 m^2. Coral colonies grow on top of rack platforms made from recycled plastic and fibergrate netting draped between PVC pipes. The racks are suspended in the water column at a depth of 1-2 meters with ropes attached to buoys at the sea surface (Fig. 1D). We studied the nursery's rack #1 in pen #1 (P1R1) and rack #1 in pen #6 (P6R1) for this project, as they both contain *M. capitata* colonies across a broad spectrum of sizes and morphologies that varied in bleaching occurrence. We measured a total of 103 *M. capitata* colonies, including 78 from P1R1 and 25 from P6R1. We conducted the photogrammetry used to create the P1R1 models on October 21, 2019 and July 29, 2021 and the photogrammetry used to create the P6R1 models on October 21, 2019 and March 30, 2021.

Fig. 1. Map showing the location of the Hawaiʻi Institute of Marine Biology (C) in Kāneʻohe Bay (B) on the island of Oʻahu, Hawaiʻi (A). The red square indicates the location of the floating coral nursery. (D) Photo of pen #1 in the nursery, where the floating docks form the outside borders of the pen, the PVC pipes form the outside borders of the racks, and the floating buoys attached to the PVC pipes are used to keep the racks at a depth of 1-2 meters. The rack in the photo is rack #1, where the spectrum of individual *M. capitata* colony size and morphology is visible. The rack is approximately 1.4 meters wide and 6.6 meters long.

Structure-from-Motion Photogrammetry

We measured coral colony dimensions from 3D models made with Structure-from-Motion (SfM) photogrammetry following the protocol outlined by Burns et al. (2015), Suka et al. (2019), and Roach et al. (2021). Briefly, we evenly distributed four to six circular marker tiles on each rack, laying them as flat as possible on top of the rack to be photographed. These tiles allow the model to be scaled in subsequent steps. While snorkeling, we photographed the corals using a

Sony A7iii camera with an 18 mm Zeiss lens positioned just below the surface of the water with a direct overhead view of the coral below. We ensured 60% overlap of consecutive photographs along the length of each rack. Once an entire rack was photographed, we captured additional images, including the underside of plating corals and lateral views of complex branching corals, to ensure we recorded the full structural complexity of each rack.

3D Model Construction

After the rack was adequately photographed, we exported all images from the camera to an Intel Core i7-4960X CPU, NVIDIA RTX 2080Ti GPU computer (Puget Systems, Auburn, WA) with 32 GB of RAM and 14 TB of storage running Ubuntu 18.04.6 with both Agisoft Metashape Professional™ (Agisoft LLC, St. Petersburg, Russia) and TagLab (Pavoni et al. 2022) software.

Metashape is designed specifically for the processing of SfM images and has been employed frequently for the construction of coral reef models (Suka et al. 2019, Lange & Perry 2020, Million & Kenkel 2020, Conley & Hollander 2021, Million et al. 2021, Miller et al. 2021, Knapp et al. 2022). We used Metashape to create and scale all components of the coral models in this study, including the 3D mesh, the 2D orthomosaic, and the digital elevation model (DEM). The program generates 3D data by analyzing gradients of light across an image to identify edges as points along a line across which these gradients diverge. The 3D mesh is a component of the model that can be rotated around X, Y, and Z axes to visualize structural complexity and 3D intricacies (Fig. 2C); the orthomosaic displays a 2D view of the model from an overhead perspective (Fig. 2A); the DEM uses either color or greyscale shading to display the 3D elevation data associated with the model (Fig. 2B). Models are scaled using the circular markers that were placed along and photographed on each rack.

Coral Measurements and Comparisons

Once a complete model was generated and scaled in Metashape, we used the image segmentation software TagLab to annotate the 2D orthomosaic (Pavoni et al. 2022; Fig. 3). We measured area and surface area for the 103 *M. capitata* coral colonies using a combination of TagLab's AI tools and manual border refinement. Once each *M. capitata* coral colony was outlined at both time points, we obtained measurements of area and surface area from the coral colony outlines and matched the colonies across the two time points to facilitate size comparisons (see protocol in Supplemental Materials).

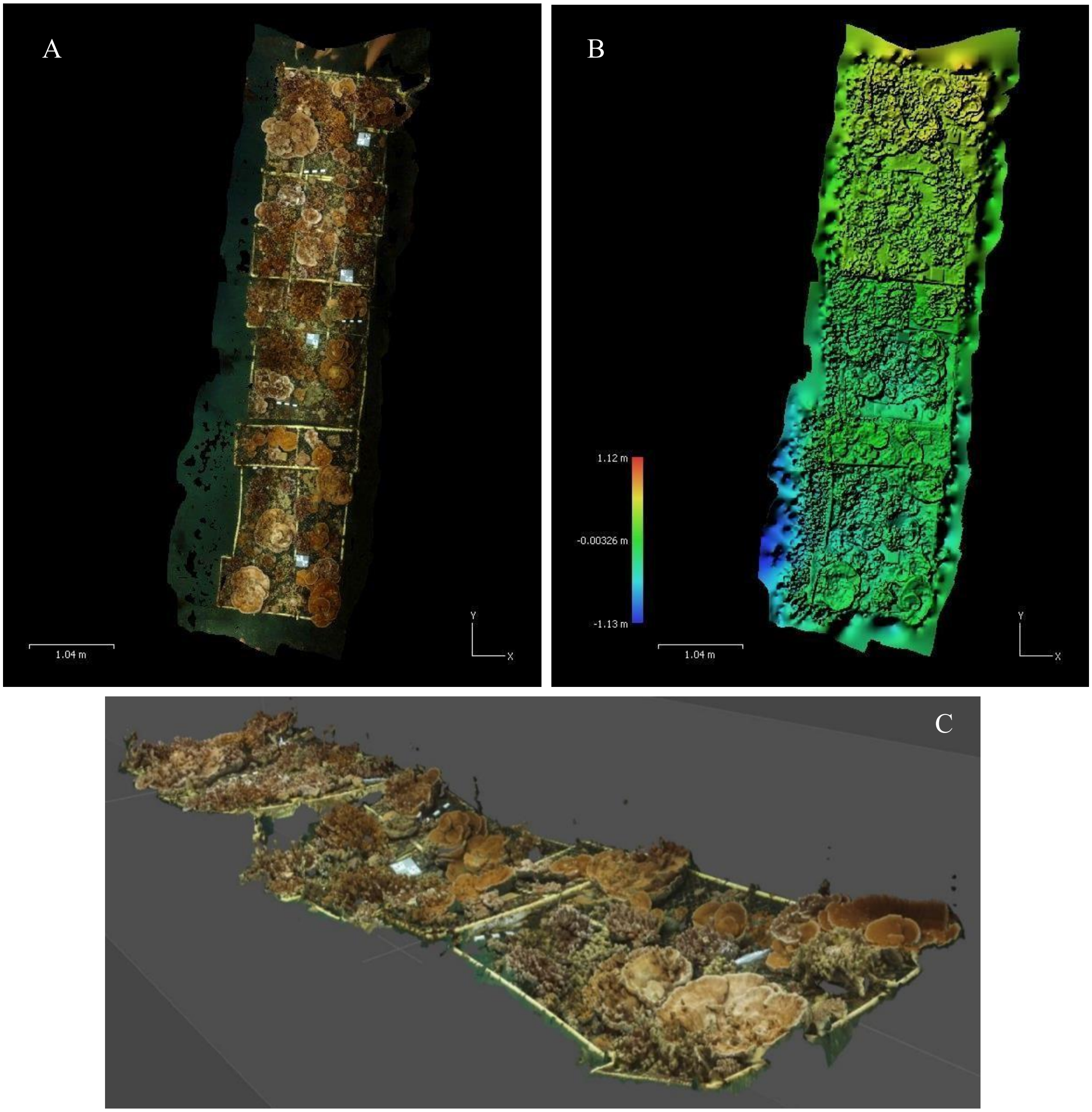

Fig. 2. (A) 2D orthomosaic in Metashape of P1R1 in the Hawaiʻi Institute of Marine Biology coral nursery. (B) Digital Elevation Model (DEM) of P1R1, where colors represent depths relative to the plane of the rack. (C) 3D mesh model of P1R1 in Metashape, shown from a different perspective to illustrate how the model can be manipulated to display 3D data. All three models were made from SfM photogrammetry taken on July 29, 2021.

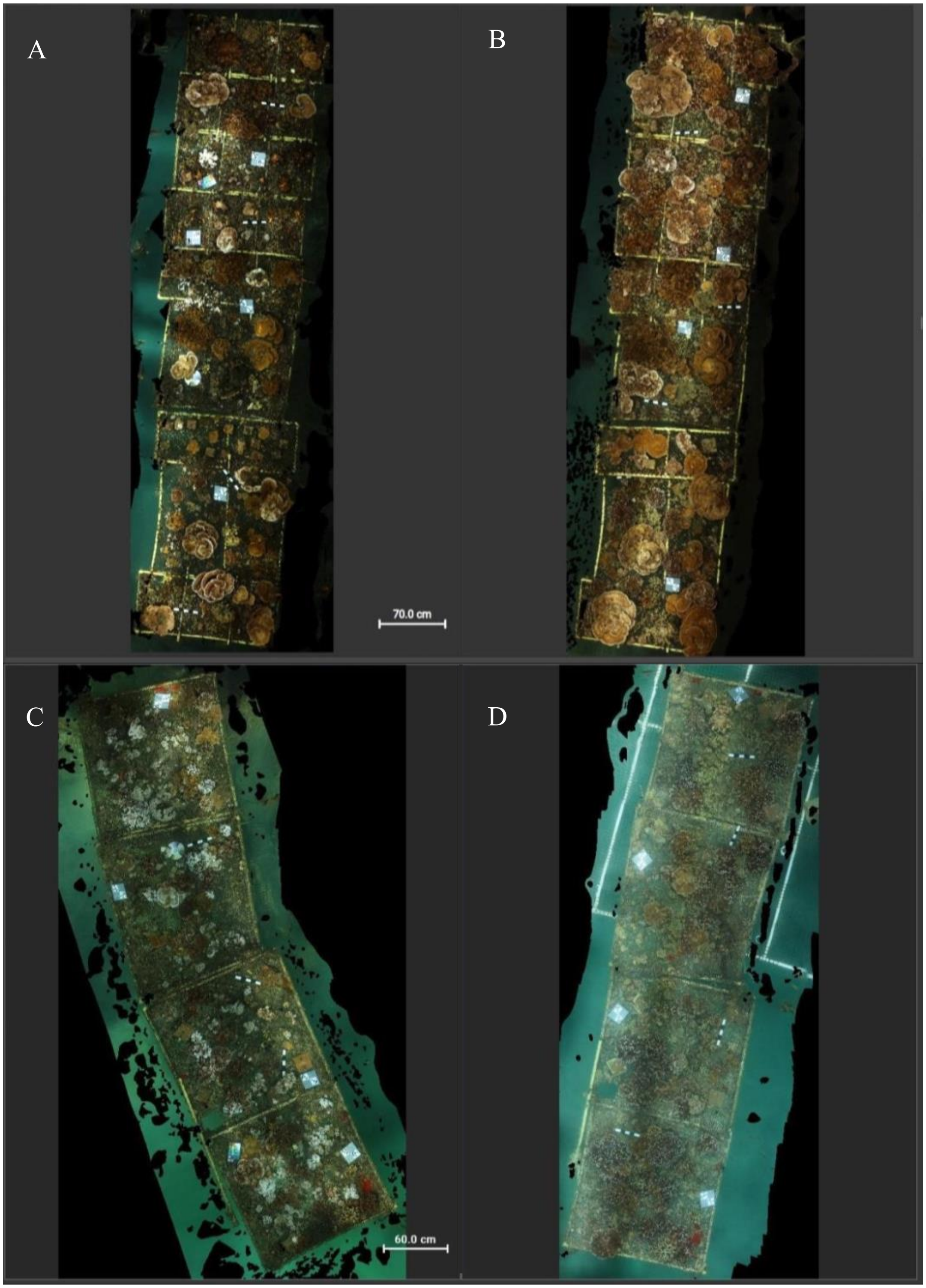

Fig. 3. TagLab split-screen displays of orthomosaics from the start (A&C) and end (B&D) points of the study. Orthomosaics were sourced from 3D models built from SfM photogrammetry P1R1 (A&B) and P6R1 (C&D) in the coral nursery.

Data Analysis

We exported measurements of area and surface area for each *M. capitata* colony at each time point into R for data analysis and used the R stats package for all analyses reported here (version 4.3.0, R Core Team 2022). We quantified morphology as surface rugosity, which is a measurement of surface roughness intended to capture the complexity of a coral's 3D structure (Young et al. 2017, Fukunaga & Burns 2020, Leon et al. 2015). We calculated surface rugosity by dividing each colony's surface area by its area. Higher rugosity values are indicative of more branching morphologies, while lower rugosity values are indicative of more plating morphologies.

We calculated the changes in *M. capitata* colony area, surface area, radius, and rugosity by subtracting the values at the first time point from the values at the second. We calculated rates of daily change in each colony's area, surface area, radius, and rugosity by dividing by the number of days that passed between the making of the two models (648 days for P1R1 and 527 days for P6R1) and then extrapolated these rates from daily change to annual change. For proportional growth rates, we scaled change in colony size by dividing by the initial colony size. We assigned each colony a bleaching score of 1 (bleached) or 0 (not bleached) by visually inspecting the orthomosaics of the racks at the first time point in 2019 when the bleaching event occurred.

To meet the statistical assumptions of all models, we performed log transformations on any variables that were not normally distributed, as assessed by the Shapiro-Wilk normality test. To determine the factors that most significantly impacted coral growth rates, we used a generalized linear model (GLM) framework to test different models using ordinary least squares. We ran 22 models assessing the linear relationships between explanatory variables (initial colony size, initial rugosity, and bleaching occurrence) and the response variable (proportional daily change), including 11 models for area and 11 models for surface area. The 11 models for each metric included a separate model for each continuous explanatory variable, a single model with all explanatory variables, and multiple models with purposeful combinations of variables and interactions between variables (Table 1). We conducted model selection using corrected Akaike's Information Criterion to account for small sample size (AICc; Akaike 1974) using the AICcmodavg package in R (Mazerolle 2023).

To assess pairwise relationships between coral colony size, rugosity, rugosity change, and growth rate, we ran linear models regressing each explanatory variable on each response variable. Specifically, we performed linear regression analyses on the following combinations of predictor and response variables: initial size and daily change in size, initial size and proportional daily change in size, initial rugosity and proportional daily change in size, initial rugosity and daily change in rugosity, initial size and daily change in rugosity, and daily change in rugosity and proportional daily change in size. We performed analyses including colony size, daily change in size, and proportional daily change in size for both area and surface area. To determine whether bleaching history affected growth rate, we performed Welch t-tests to compare the proportional daily change in both area and surface area between bleached and unbleached coral colonies.

Results

Across all *M. capitata* colonies, proportional daily change in area was highly correlated with the proportional daily change in surface area ($t = 46.18$, $df = 100$, $p < 0.01$, $r = 0.98$), and both response variables were significantly affected in the same manner by each predictor variable. Therefore, *M. capitata* growth rate can be quantified with either area or surface area (SA) measurements to yield statistical comparisons with similar results. Due to the better capacity of SA measurements to capture coral colony shape and size in 3D compared to 2D area measurements, we only discuss measures of growth in surface area here but include area results in the supplemental materials.

The 103 *M. capitata* corals measured in this study exhibited a wide range of growth rates, with colonies increasing in SA from a minimum of 0 cm^2 per day to a maximum of 3.7 cm^2 per day (1300 cm^2 per year). Proportional growth rates relative to initial colony SA also varied widely, with annual change ranging from a minimum of 0% to a maximum of 1100%. These large ranges contributed to large errors (+/- SD) that sometimes exceeded the mean values. On average, corals increased in SA by a mean of 0.9 cm^2 (+/- 0.8 SD) per day (320 cm^2 (+/- 270 SD) per year). Relative to initial colony size, proportional growth rates of *M. capitata* SA averaged 0.56% (+/- 0.60 SD) per day (210% (+/- 220 SD) per year).

Model Selection

The best model for explaining proportional growth in SA based on the corrected Akaike Information Criterion (AICc) included initial size and bleaching occurrence as predictors (Fig. 4) and carried 60% of the cumulative model weight (Fig. 4, Table 1). The predictors for the second-best model also included initial size and bleaching occurrence, but with the addition of the interaction between these two factors. This model had a delta AICc of 2.19 and carried an additional 19% of the cumulative model weight. The predictors for the third-ranking model again included initial size and bleaching occurrence, but with the addition of initial rugosity. This model had a delta AICc of 2.21 and carried an additional 20% of the cumulative model weight. Altogether, these top three ranking models encompassed 99% of the predictive power of the models explaining proportional growth in SA (Table 1).

Table 1. AICc results for linear models predicting proportional daily change in surface area (SA). For each model: K represents the number of estimated parameters; AICc represents the corrected Akaike Information Criterion; Delta AICc represents the difference in AICc between each model and the model with the lowest AICc; AICc Wt represents the model's weight or probability of being the best model; Cum. Wt represents the cumulative model weights; and LL represents the log-likelihood of the model. In the variables column, SA1 represents initial surface area and R1 represents initial rugosity.

Variables	**K**	**AICc**	**Delta AICc**	**AICc Wt**	**Cum. Wt**	**LL**
SA1 + bleach	4	189.65	0.00	0.60	0.60	-90.62
SA1 + bleach + interaction	5	191.84	2.19	0.19	0.79	-90.61
SA1 + R1 + bleach	5	191.86	2.21	0.20	0.99	-90.62
SA1 + R1 + bleach + interactions	8	198.26	8.62	0.01	1.00	-90.36
SA1	3	212.81	23.16	0.00	1.00	-103.28
SA1 + R1	4	214.84	25.19	0.00	1.00	-103.21
SA1 + R1 + interaction	5	217.04	27.40	0.00	1.00	-103.21
R1 + bleach	4	291.12	101.48	0.00	1.00	-141.36
R1 + bleach + interaction	5	292.87	103.22	0.00	1.00	-141.12
R1	3	296.14	106.50	0.00	1.00	-144.95
bleach	3	303.37	113.73	0.00	1.00	-148.56

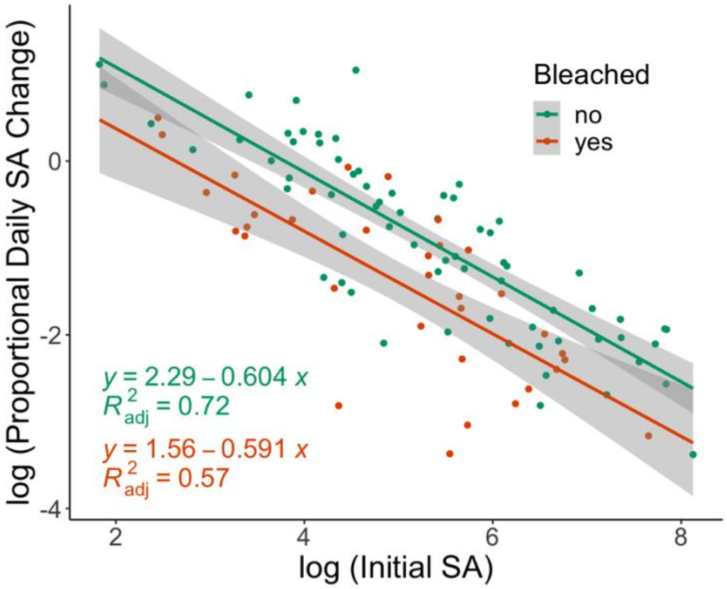

Fig. 4. Scatterplot depicting the significant negative linear relationship between log-transformed initial *M. capitata* colony size and log-transformed proportional daily growth rate in surface area (SA; $p < 0.01$). The red points and red best-fit lines represent colonies that bleached, while green points and green best-fit lines represent colonies that did not bleach. The shaded regions around best-fit lines represent the 95% confidence intervals.

Coral Size & Growth

Initial coral SA ranged from 6.21 cm^2 to 3380 cm^2, and the distribution was skewed to larger colonies, with a median of 225 cm^2 and a mean of 450 cm^2. The initial SA for 73% of the corals was less than the mean, so most corals in this study began small. Initial colony size was a significant predictor of *M. capitata* growth rate. Specifically, there was a significant positive linear relationship between the log of initial SA and the log of daily SA change ($R^2 = 0.45$, $F(1,100) = 83.76$, $p < 0.01$; Fig. 5A). Alternatively, there was a significant negative linear relationship between the log of initial SA and the log of proportional daily SA change ($R^2 = 0.60$, $F(1,100) = 153.70$, $p < 0.01$; Fig. 5B). These relationships indicate that, compared to larger corals, smaller colonies experienced relatively smaller increases in total SA but relatively larger increases in proportional SA. Overall, however, colonies grew at relatively constant rates across colony sizes (Figs. S2 & S3).

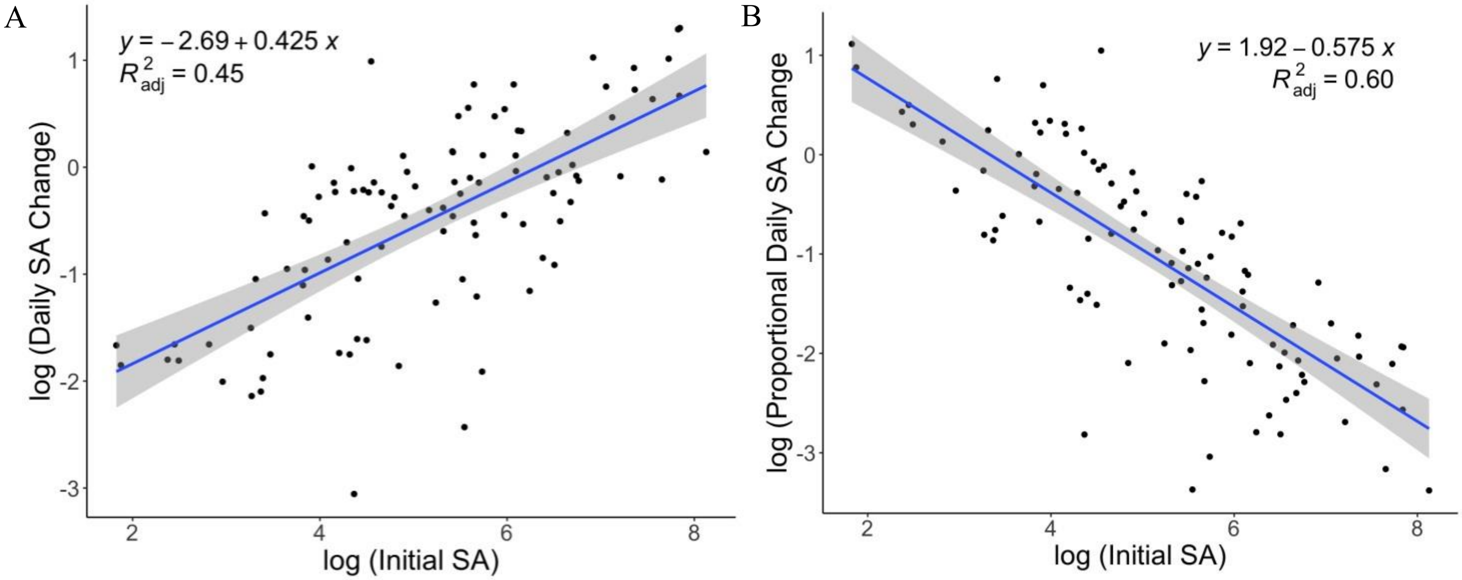

Fig. 5. Scatterplots depicting the relationships between initial *M. capitata* colony size and daily growth. The shaded area around the best-fit lines represents the 95% confidence interval. (A) Significant positive linear relationship between log-transformed initial colony surface area (SA) and daily change in SA ($p < 0.01$). (B) Significant negative linear relationship between log-transformed initial colony SA and proportional daily change in SA ($p < 0.01$).

Coral Rugosity & Growth

Initial rugosity was a significant predictor of *M. capitata* colony growth rate. Rugosity analyses were performed on log-transformed growth rate data and untransformed rugosity data because the raw rugosity data met all statistical assumptions. There was a significant negative linear relationship between initial rugosity and the log of proportional daily change in SA ($R^2 = 0.10$, $F(1,100) = 12.05$, $p < 0.01$; Fig. 6A). Although the explanatory power of this linear relationship was low, it indicates that less rugose (more plate-like) *M. capitata* colonies grow faster than more rugose (more branched) colonies based on their proportional increases in SA.

Mean rugosity was significantly greater in 2021 than in 2019, increasing by 1.08-fold from 1.96 (+/- 0.342 SD) in 2019 to 2.11 (+/- 0.340) in 2021 ($t(102) = -4.832$, $p < 0.01$; Fig. 7A). However, 30% of the corals decreased in rugosity over this time, and overall, 42% of colonies fell within one standard deviation of zero change (Fig. 7B). Initial rugosity was a significant predictor of rugosity change, where coral colonies with lower initial rugosity experienced greater changes in rugosity over time than colonies with higher initial rugosity ($R^2 = 0.21$, F(1,101) = 27.25, $p < 0.01$; Fig. 7B).

Smaller corals exhibited greater daily changes in rugosity than larger corals based on their initial SA, indicated by the significant negative linear relationship between daily rugosity change and the log of initial colony SA ($R^2 = 0.19$, F(1,101) = 25.47, $p < 0.01$; Fig. 7C). Additionally, corals that grew more, as evidenced by larger proportional daily changes in SA, also experienced greater daily increases in rugosity, indicated by a significant positive linear relationship between daily rugosity change and the log of proportional daily change in SA ($R^2 = 0.23$, F(1,100) = 30.36, $p < 0.01$; Fig. 6B). This positive relationship between rugosity change and growth rate follows from the aforementioned results that smaller corals grow proportionally faster and experience greater changes in rugosity than larger corals.

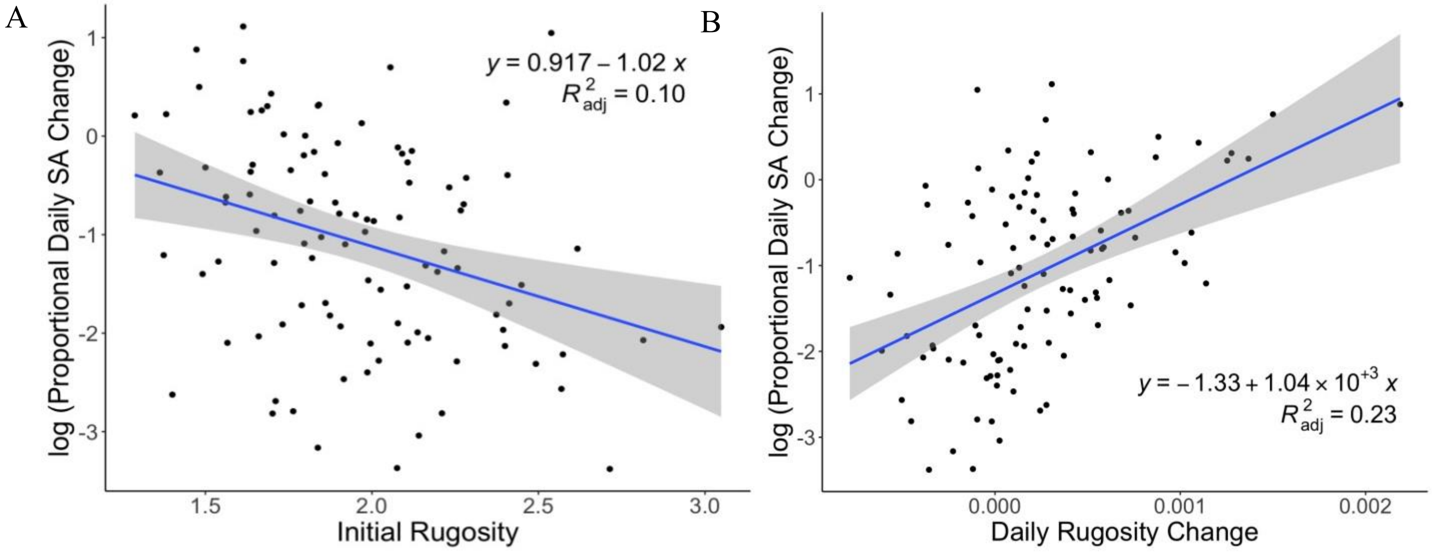

Fig. 6. Scatterplots depicting (A) the significant negative linear relationship between initial *M. capitata* colony rugosity and log-transformed proportional daily growth rate in surface area (SA; $p < 0.01$) and (B) the significant positive linear relationship between daily change in *M. capitata* colony rugosity and log-transformed proportional daily growth rate in SA ($p < 0.01$). The shaded area around the best-fit lines represents the 95% confidence interval.

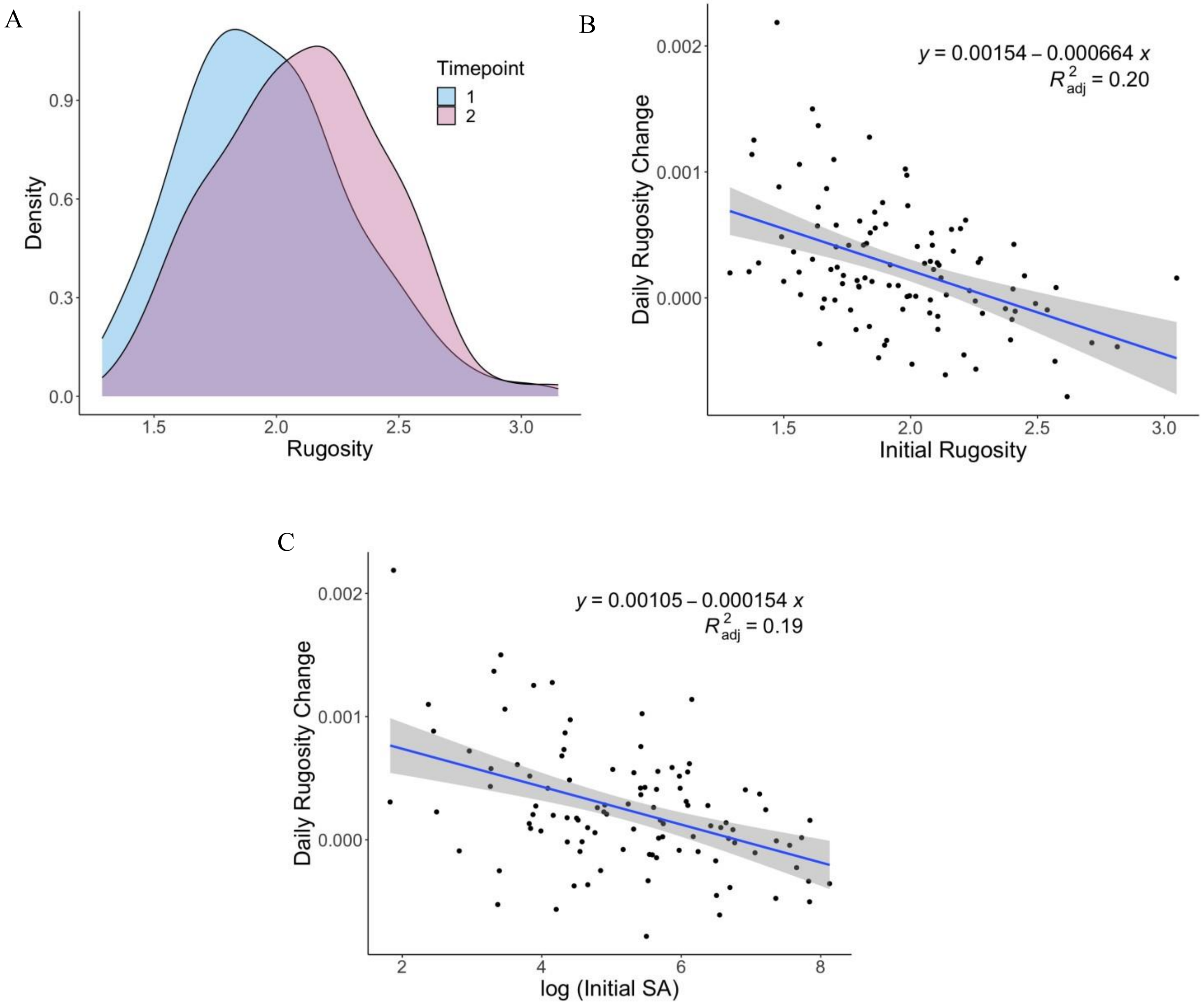

Fig. 7. (A) Density curves depicting the shift in distribution of rugosities of *M. capitata* colonies from the first time point to the second. (B) Scatterplot depicting the significant negative linear relationship between initial colony rugosity and daily change in rugosity ($p < 0.01$). (C) Scatterplot depicting the significant negative linear relationship between log-transformed initial colony size in surface area (SA) and daily change in *M. capitata* colony rugosity ($p < 0.01$). The shaded regions around the best-fit lines represent the 95% confidence interval.

Coral Bleaching & Growth

We leveraged the bleaching event in 2019 to include 35 *M. capitata* colonies that exhibited visual bleaching at the first time point of this study in 2019. All of these corals survived and had recovered completely by 2021. Corals that bleached in 2019 increased in SA by an average of 0.39% (+/- 0.38 SD) per day (140% (+/- 140 SD) per year), while corals that did not bleach increased in SA by an average of 0.65% (+/- 0.67 SD) per day (240% (+/- 240 SD) per year). Bleaching occurred among a variety of sizes and morphologies of corals, resulting in a considerable range of growth rates among these groups; variation equaled or exceeded the mean estimates of proportional daily change in SA (Fig. 4). Despite this variation, bleached colonies grew significantly slower than colonies that did not bleach. Proportional daily growth in SA was 1.67 fold lower for bleached corals than for corals that showed no visible signs of bleaching (student's t(100) = 2.094, p = 0.0388; Fig. 4).

Discussion

In this study, we used 3D Structure-from-Motion (SfM) photogrammetry to document the growth rate of 103 *M. capitata* coral colonies over 21 months from October 2019 to July 2021. We quantified growth rate as both change in planar area and change in surface area to account for 2D and 3D growth in each coral colony, since *M. capitata* growth occurs along a spectrum from flat 2D plates to complex 3D branches. Here we discuss growth rate in terms of proportional change in surface area since this metric more comprehensively captures colony growth in all three dimensions, and both measures were highly correlated. Quantifying and analyzing changes in coral colony size and rugosity over the course of this study indicated that colony size, rugosity, and recent bleaching history were all significant predictors of *M. capitata* growth rate.

Coral Size & Growth

Absolute growth rate of *Montipora capitata* increased with increasing colony size, but proportional growth rate based on initial colony size decreased with increasing colony size. These trends are the result of constant rates of linear growth across *M. capitata* colony sizes (Figs S2 & S3). Constant linear growth rate across colony sizes creates a negative trend in proportional SA growth rate with colony size because as colony size increases, the constant increment of linear growth becomes increasingly smaller relative to total colony size. Similarly, constant linear growth rate across colony sizes creates a positive trend in total SA growth rate with colony size because as colony size increases, the constant increment of linear growth creates increasingly larger rates of growth in SA as colony size increases. Constant growth rates are characteristic of colonial organisms, like corals, that grow indeterminately by continuing to increase in size at a constant rate even as they get larger (Winston 2010).

Decreasing proportional growth rate with increasing colony size is consistent with many other studies that assessed coral growth over time (Hughes and Jackson 1985, Hughes and Connell 1987, Kim and Lasker 1998) and matches the expectation of an allometric growth model (Dornelas et al. 2017, Madin et al. 2020, Million et al. 2021). In *M. capitata,* larger corals have more initial area to grow from and can therefore increase their total size more quickly than smaller corals, but larger corals may exhibit slower proportional growth rates relative to smaller corals (Kim and Lasker 1998, Dornelas et al. 2017) due to differences in resource capture compared to smaller corals (Jokiel and Morrissey 1986). Additionally, faster proportional growth rates in small colonies may be a mechanism to avoid higher incidences of mortality associated with smaller colony size (Hughes and Jackson 1985, Madin et al. 2014, Forsman et al. 2020, Kodera et al. 2020, Madin et al. 2020).

Coral Rugosity & Growth

Montipora capitata morphology is highly phenotypically plastic relative to other coral species (McLachlan et al. 2021), making it challenging to objectively draw a boundary between different morphologies (Forsman et al. 2010; Cunha et al. 2019). We used surface rugosity, calculated as the ratio of 3D surface area to 2D planar area, to quantitatively characterize colony morphology on the spectrum from plating (lower rugosity) to branching (higher rugosity) and provide a discrete rugosity value for each coral. Average *M. capitata* rugosity across all colonies increased over time (Fig. 7A), but the magnitude and direction of rugosity change varied among colonies (Fig. 7B). Rugosity increased for 70% of colonies and decreased for 30%, and the magnitude of change in either direction was within one standard deviation of zero for 42% of the colonies. In general, smaller corals experienced greater increases in rugosity than larger corals did (Fig. 7D), and corals that were less rugose at the start of the study (plating forms) experienced greater increases in rugosity than corals that were more rugose at the start of the study (branching forms; Fig. 7C). Additionally, colonies that experienced larger increases in rugosity grew faster than colonies that experienced smaller increases in rugosity (Fig. 6B).

Taken together, these results indicate that *M. capitata* corals generally become more rugose as they grow, which supports evidence that coral surface complexity increases with colony size (Zawada et al. 2019, Madin et al. 2020). This increase in rugosity could be the result of growth in the relatively high-light, low wave action environment of the HIMB coral nursery, as these conditions promote the growth of more branching morphologies (Chappell 1980). Additionally, corals may become more rugose and direct their growth upwards rather than outwards due to the likelihood of competition for space and light with neighboring colonies as they become larger (George et al. 2021; Fig. S8).

We found a significant relationship between *M. capitata* morphology and growth rate. Specifically, less rugose colonies (plating morphs) grew faster than more rugose colonies (branching morphs; Fig. 6A). This result is consistent with other studies that measured growth rate across morphological groups consisting of different species (Dornelas et al. 2017, Madin et al. 2020) but is the first report we know of for variation in growth rate across a gradient of morphologies within a single species. Compared to branching morphologies, the faster growth of plating *M. capitata* morphologies may be a result of their ability to better capture light and resources for symbiont photosynthesis, providing them with more energy for skeletal growth (Kim and Lasker 1998, Muko et al. 2000, Zawada et al. 2019).

Recent Bleaching History & Growth

Corals that were bleached during the first time point of this study (2019) grew a mean of 1.67 times slower than corals that did not bleach during the study. Bleaching has led to decreased growth rates in other species and locations, such as in *Porites* colonies on the Great Barrier Reef (Cantin & Lough 2014), *Acropora* corals in American Sāmoa (Gold & Palumbi 2018), and *Montastrea* corals in Jamaica (Goreau and Macfarlane 1990). However, coral growth rates are not always negatively impacted by bleaching; growth rates of *Acropora* on the Great Barrier Reef, for example, were largely independent of bleaching severity (Baird & Marshall 2002), and growth rates of some long-lived *Porites* corals in the Red Sea increased after a severe bleaching event (Mantanona & DeCarlo 2023). Interspecific variation in bleaching severity and recovery (McCowan et al. 2012, Razak et al. 2020) may explain the variation between our results and the results of previous studies, while intraspecific variation in heat resistance and growth rate after bleaching (Goreau and Macfarlane 1990, Gold and Palumbi 2018) may account for the differences in growth rate between bleached and unbleached *M. capitata* colonies observed within this study. However, additional long-term physiological effects of bleaching, such as the reduction of coral reproductive rates (Johnston et al. 2020), and complex trade-offs between growth rate and bleaching resistance (Walker et al. 2023) make it difficult to identify the cause of differences in growth rate recovery after coral bleaching.

We did not find a significant interaction between size and bleaching or between rugosity and bleaching with respect to growth rate in *M. capitata*. Colony size (Johnston et al. 2020, Speare et al. 2022, Kopecky et al. 2023) and morphology (McCowan et al. 2012, Muko et al. 2013, Mattan-Moorgawa et al. 2018, Sakai et al. 2019) both influence corals' ability to resist and survive bleaching. However, despite evidence for tradeoffs between coral size and morphology with regards to bleaching susceptibility and mortality (Speare et al. 2022, Kopecky et al. 2023, Muko et al. 2013, Mattan-Moorgawa et al. 2018, Sakai et al. 2019, Lange et al. 2023), our results indicate that growth rate after bleaching is not correlated with either colony size or morphology in *M. capitata* corals. While coral size and morphology have previously been shown to affect recovery from bleaching (Lange et al. 2023), we conclude that there are no obvious tradeoffs between size, morphology, and post-bleaching growth rate in the *M. capitata* colonies studied here. More research is necessary to quantify if and how individual coral colonies continue to grow after bleaching to scrutinize these different findings and improve our understanding of post-bleaching coral recovery (McLachlan et al. 2020).

Conclusion

This study illustrates the use of 3D photogrammetry for quantifying the impacts of colony size, morphology, and bleaching history on *M. capitata* growth rates in a coral nursery in Kāneʻohe Bay. Small corals, less rugose corals, and corals with no history of bleaching grew the fastest, experiencing the greatest changes in both area and surface area. These data inform coral reef management and restoration initiatives that aim to quickly increase coral cover by identifying small and plating colonies as the fastest-growing corals for breeding and outplanting. Additionally, this study establishes a new baseline for *M. capitata* coral growth against which future studies can be compared to track growth rates through time and understand how individual colonies respond to and recover from subsequent disturbances. The methods we use provide an open-source, standardizable approach for quantifying coral growth and rugosity, proven in a species whose phenotypic plasticity is exceptional and challenging to measure or objectively separate into morphological groups. Expanding this approach to additional coral species and locations will enable these inferences to be extrapolated to the reef scale, which will allow larger-scale monitoring of coral populations and their ability to resist and recover from ongoing anthropogenic disturbances and bleaching events.

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APPENDICES

Appendix 1: Area Results

The 103 *M. capitata* corals measured in this study exhibited a wide range of growth rates, with colonies increasing in area from a minimum of 0 cm^2 per day to a maximum of 2.4 cm^2 per day (880 cm^2 per year). Proportional growth rates relative to initial colony area also varied widely, with annual change ranging from a minimum of 0% to a maximum of 1100%. These large ranges contributed to large errors (+/- SD) that sometimes exceeded the mean values. On average, corals increased in area by a mean of 0.4 cm^2 (+/- 0.4 SD) per day (150 cm^2 (+/- 140 SD) per year). Relative to initial colony size, proportional growth rates of *M. capitata* area averaged 0.48% (+/- 0.50 SD) per day in area (180% (+/- 180 SD) per year).

Model Selection

The best model for explaining proportional growth in area (based on the corrected Akaike Information Criterion (AICc)) included initial size and bleaching occurrence as predictors (Fig. S1) and carried 60% of the cumulative model weight (Table S1). The predictors for the second-best model also included initial size and bleaching occurrence, but with the addition of the interaction between these two factors. This model had a delta AICc of 2.20 and carried an additional 19% of the cumulative model weight. The predictors for the third-ranking model again included initial size and bleaching occurrence, but with the addition of initial rugosity. This model had a delta AICc of 2.21 and carried an additional 20% of the cumulative model weight. Altogether, these top three ranking models encompassed 99% of the predictive power of the models explaining proportional growth in area (Table S1).

Table S1. AICc results for linear models predicting proportional daily change in area. For each model: K represents the number of estimated parameters; AICc represents the corrected Akaike Information Criterion; Delta AICc represents the difference in AICc between each model and the model with the lowest AICc; AICc Wt represents the model's weight or probability of being the best model; Cum. Wt represents the cumulative model weights; and LL represents the loglikelihood of the model. In the variables column, A1 represents initial area and R1 represents initial rugosity.

Variables	**K**	**AICc**	**Delta AICc**	**AICc Wt**	**Cum. Wt**	**LL**
A1 + bleach	4	184.30	0.00	0.60	0.60	-87.94
A1 + bleach + interaction	5	186.50	2.20	0.19	0.79	-87.94
A1 + R1 + bleach	5	186.51	2.21	0.20	0.99	-87.94
A1 + R1 + bleach + interactions	8	192.85	8.55	0.01	1.00	-87.65
A1	3	206.17	21.87	0.00	1.00	-99.96
A1 + R1	4	208.17	23.87	0.00	1.00	-99.88
A1 + R1 + interaction	5	210.18	25.88	0.00	1.00	-99.78
R1 + bleach	4	281.33	97.03	0.00	1.00	-136.46
R1 + bleach + interaction	5	282.93	98.63	0.00	1.00	-136.15
R1	3	286.12	101.82	0.00	1.00	-136.94
bleach	3	286.88	102.58	0.00	1.00	-140.32

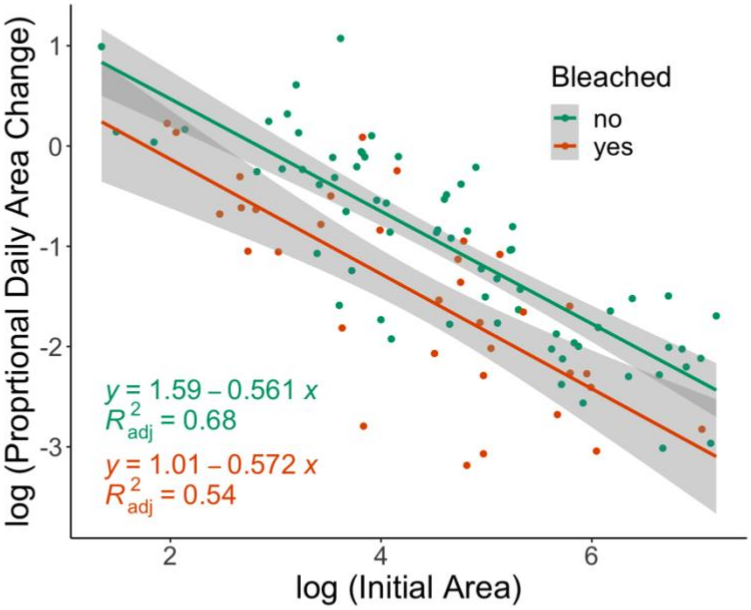

Fig. S1. Scatterplot depicting the significant negative linear relationship between log-transformed initial *M. capitata* colony size and log-transformed proportional daily growth rate in area ($p < 0.01$). The red points and red best-fit lines represent colonies that bleached, while green points and green best-fit lines represent colonies that did not bleach. The shaded regions around best-fit lines represent the 95% confidence intervals.

Coral Size & Growth

Initial coral area ranged from 3.85 cm^2 to 1310 cm^2, and the distribution was positively skewed to the right with a median of 105 cm^2 and a mean of 217 cm^2. The initial area of 87% of the corals was less than the mean, so the majority of corals were small. Initial colony size was a significant predictor of *M. capitata* growth rate. Specifically, there was a significant positive linear relationship between the log of initial area and the log of daily area change ($R^2 = 0.48$, $F(1,100) = 94.89$, $p < 0.01$; Fig. S2B). Alternatively, there was a significant negative linear relationship between the log of initial area and the log of proportional daily area change ($R^2 = 0.56$, $F(1,100) = 131.80$, $p < 0.01$; Fig. S3B). These relationships indicate that, compared to larger corals, smaller colonies experienced relatively smaller increases in total area but relatively larger increases in proportional area. However, theoretical lines of constant linear growth fall mostly within the margin of error (grey shading) of the best-fit lines for the data, indicating that the *M. capitata* colonies in this study grew at relatively constant linear rates across colony sizes (Figs. S2 & S3). Estimates of constant linear growth rate were derived from converting area to radius and then back to area, which does not fully represent three-dimensional colony growth in the same way that surface area (SA) does (especially for more complex branching colonies). The mathematical constraints of converting colony size to radius for this analysis prevented us from doing a similar analysis for SA.

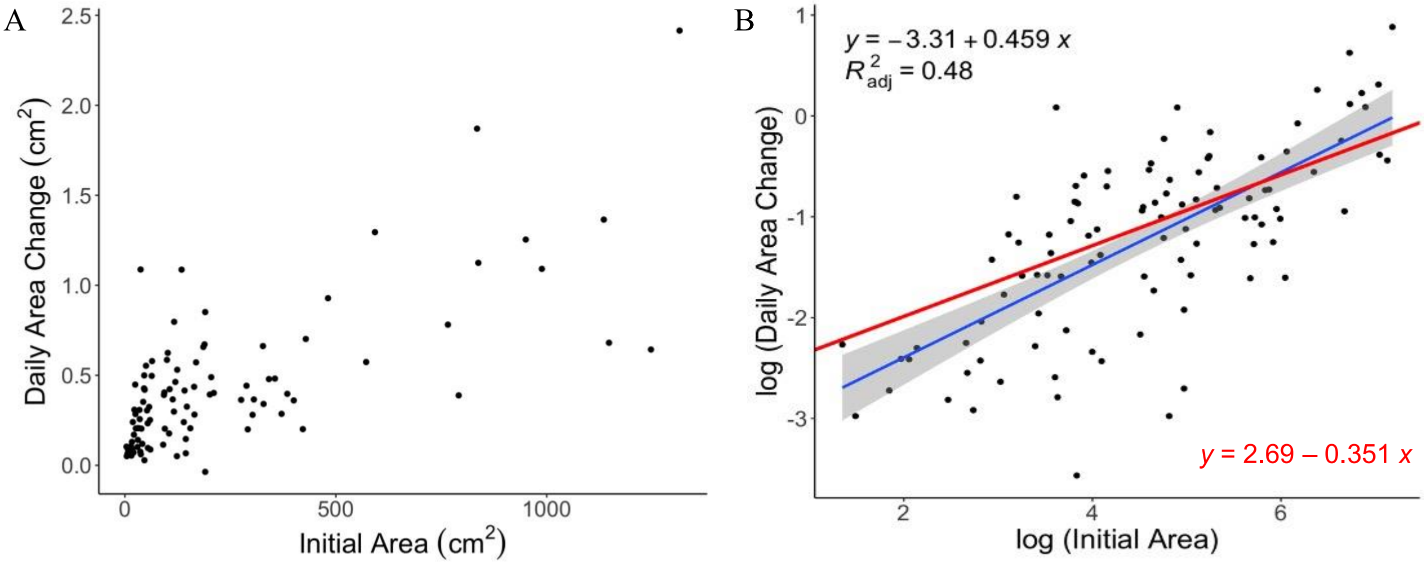

Fig. S2. Scatterplots depicting the relationships between initial *M. capitata* colony size and daily growth. (A) Relationship between initial colony area and daily change in area. (B) Significant negative linear relationship between log-transformed initial colony area and proportional daily change in area ($p < 0.01$). The shaded area around the blue best-fit line represents the 95% confidence interval. The red line represents theoretical daily growth in area if all colonies grew in constant radial increments of 0.0067 cm per day, which was the average daily radial growth rate across all colony sizes when area was converted to radius.

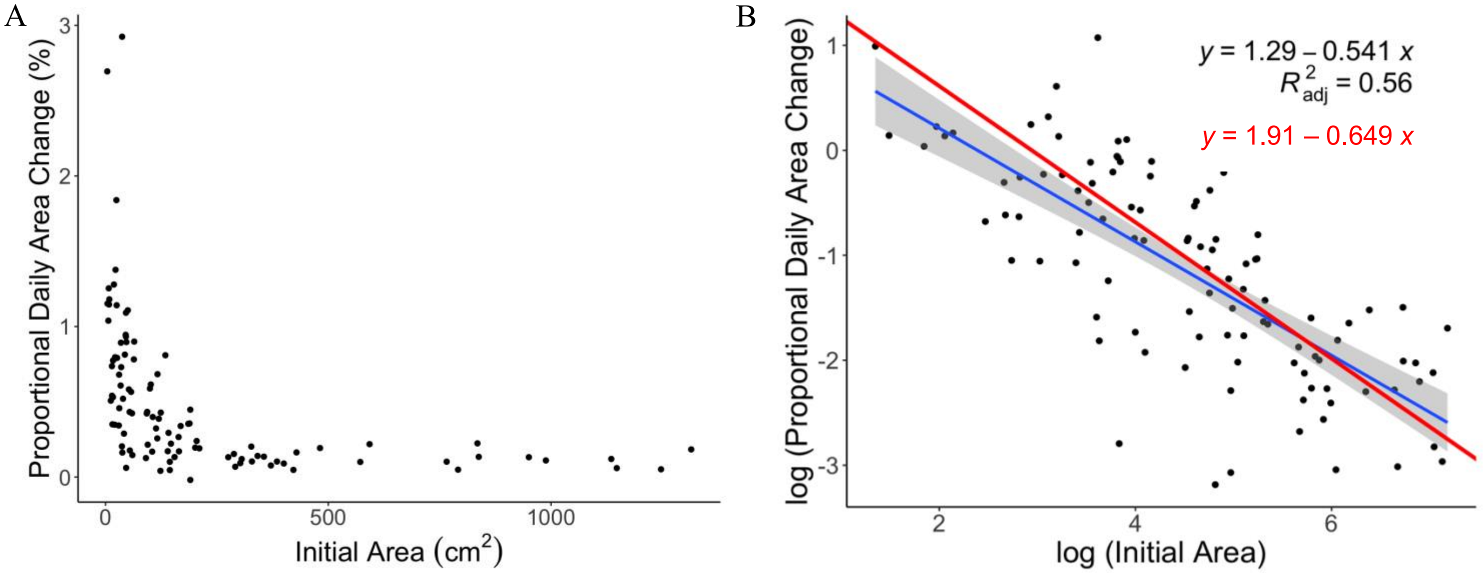

Fig. S3. Scatterplots depicting the relationships between initial *M. capitata* colony size and proportional daily growth, scaled by initial colony size. (A) Relationship between initial colony area and proportional daily change in area. (B) Significant negative linear relationship between log-transformed initial colony area and proportional daily change in area ($p < 0.01$). The shaded area around the blue best-fit line represents the 95% confidence interval. The red line represents theoretical daily growth in area if all colonies grew in constant radial increments of 0.0067 cm per day, which was the average daily radial growth rate across all colony sizes when area was converted to radius.

Coral Rugosity & Growth

Initial rugosity was a significant predictor of *M. capitata* colony growth rate. Rugosity analyses were performed on log-transformed growth rate data and untransformed rugosity data, since the raw rugosity data met all statistical assumptions. There was a significant negative linear relationship between initial rugosity and the log of proportional daily change in area ($R^2 = 0.046$, $F(1,100) = 5.842$, $p = 0.0175$; Fig. S4A). Although the explanatory power of this linear relationship was low, it indicates that less rugose (more plate-like) *M. capitata* colonies grow faster than more rugose (more branched) colonies based on their relative proportional increases in area.

Smaller corals exhibited greater daily changes in rugosity than larger corals based on their initial area, indicated by the significant negative linear relationship between daily rugosity change and the log of initial colony area ($R^2 = 0.16$, $F(1,101) = 20.64$, $p < 0.01$; Fig. S4C). Additionally, corals that grew more, as evidenced by larger proportional daily changes in area, also experienced greater daily increases in rugosity, indicated by a significant positive linear relationship between daily rugosity change and the log of proportional daily change in area ($R^2 = 0.081$, $F(1,100) = 9.893$, $p < 0.01$; Fig. S4B). This positive relationship between rugosity change and growth rate follows from the aforementioned results that smaller corals grow proportionally faster and experience greater changes in rugosity than larger corals.

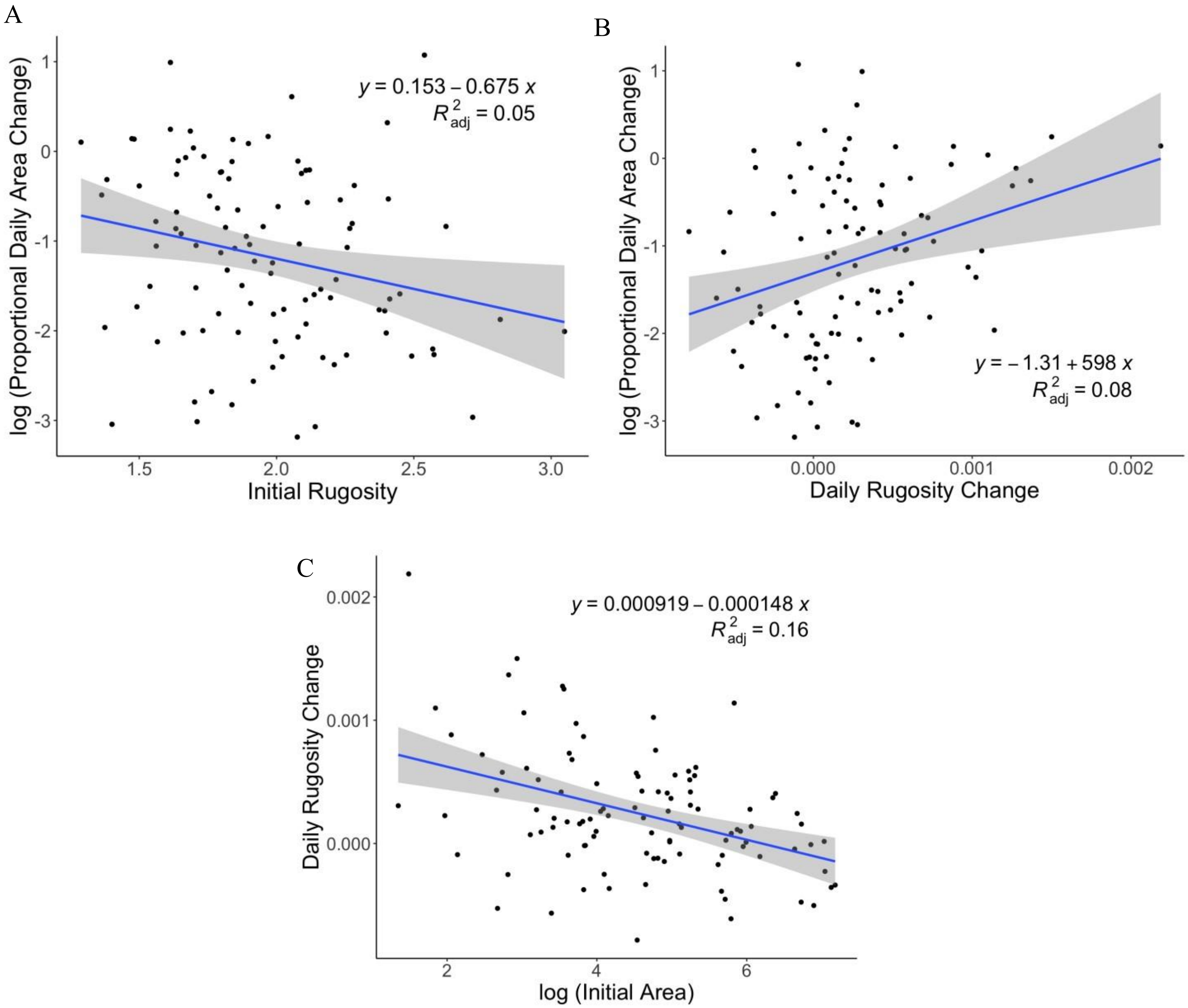

Fig. S4. Scatterplots depicting (A) the significant negative linear relationship between initial *M. capitata* colony rugosity and log-transformed proportional daily growth rate in area ($p < 0.01$), (B) the significant positive linear relationship between daily change in *M. capitata* colony rugosity and log-transformed proportional colony growth rate in area ($p < 0.01$), and (C) the significant negative linear relationship between log-transformed initial colony size in area and daily change in *M. capitata* colony rugosity ($p < 0.01$). The shaded area around the best-fit lines represents the 95% confidence interval.

Coral Bleaching & Growth

We leveraged the bleaching event in 2019 to select 35 *M. capitata* colonies that exhibited visual bleaching at the first time point of this study in 2019. All of these corals survived and had recovered by 2021. Corals that bleached in 2019 increased in area by an average of 0.34% (+/- 0.33 SD) per day (130% (+/- 120 SD) per year), while corals that did not bleach increased in area by an average of 0.56% (+/- 0.56 SD) per day (200% (+/- 200 SD) per year). Bleaching occurred among a variety of sizes and morphologies of corals, resulting in a considerable range of growth rates among these groups, with variation equaling or exceeding the mean estimates of proportional daily change in area (Fig. S5). Despite this variation, bleached colonies grew significantly slower than colonies that did not bleach. Proportional daily growth in area was 1.65 fold lower for bleached corals than for corals that did not bleach (student's t(100) = 2.247, p = 0.0268; Fig. S5).

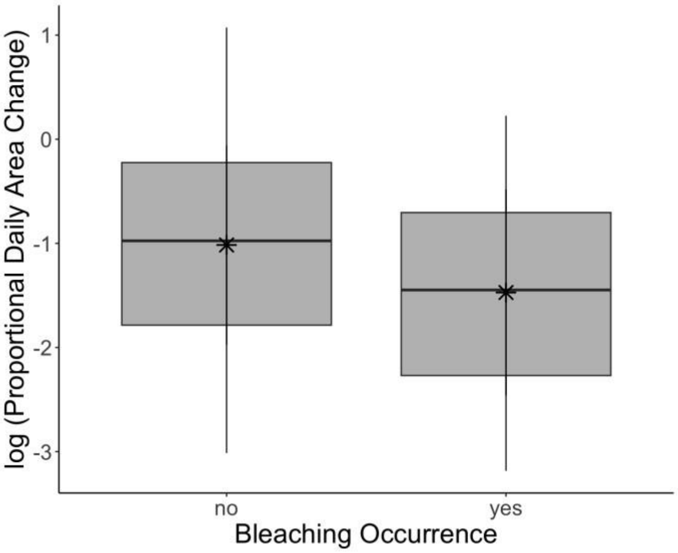

Fig. S5. Boxplot comparing mean log-transformed proportional daily growth rates in area for *M. capitata* coral colonies with and without evidence of bleaching. Stars represent the means, bold horizontal lines represent the medians, horizontal bounds of the boxes represent the upper (75th) and lower (25th) quartiles, and vertical lines represent standard deviation.

Appendix 2: Surface Area Results

Coral Size & Growth

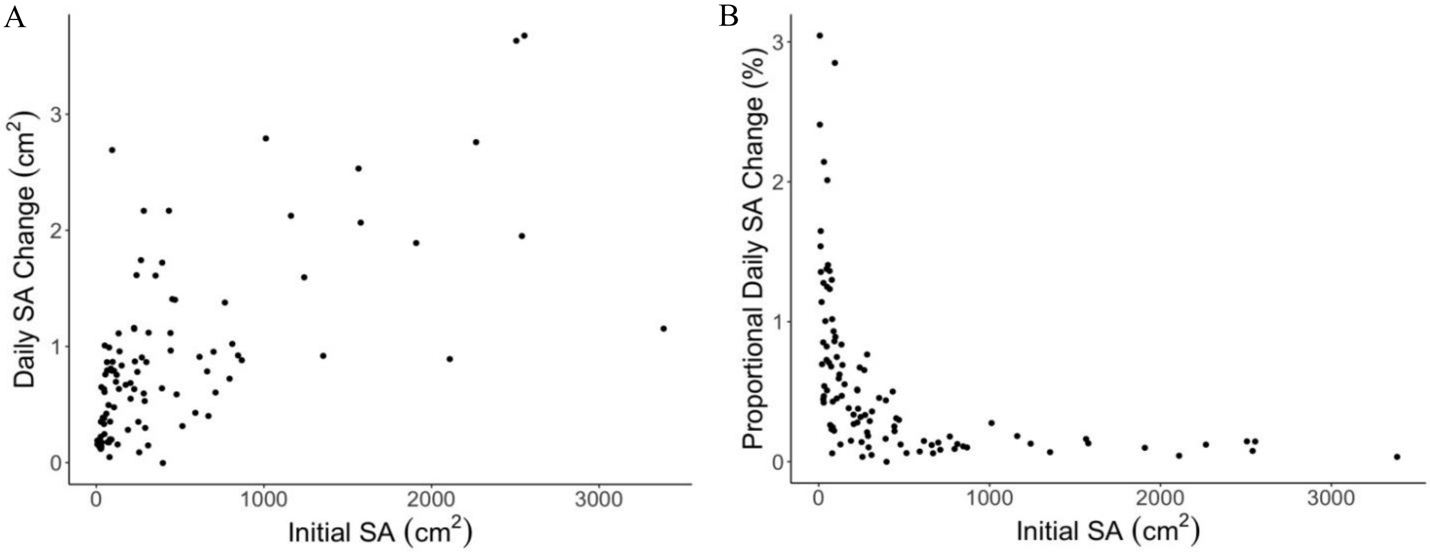

Fig. S6. Scatterplots depicting the relationships between initial *M. capitata* colony size and daily growth. The shaded area around the best-fit lines represents the 95% confidence interval. (A) Relationship between initial colony surface area (SA) and daily change in SA. (B) Relationship between initial colony SA and proportional daily change in SA.

Coral Bleaching & Growth

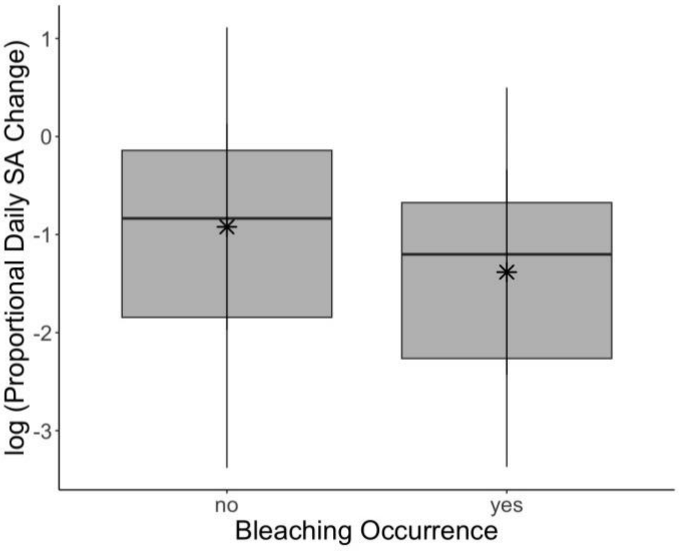

Fig. S7. Boxplot comparing mean log-transformed proportional daily growth rates in surface area (SA) for *M. capitata* coral colonies with and without evidence of bleaching. Stars represent the means, bold horizontal lines represent the medians, horizontal bounds of the boxes represent the upper (75th) and lower (25th) quartiles, and vertical lines represent standard deviation.

Colony Contact & Growth

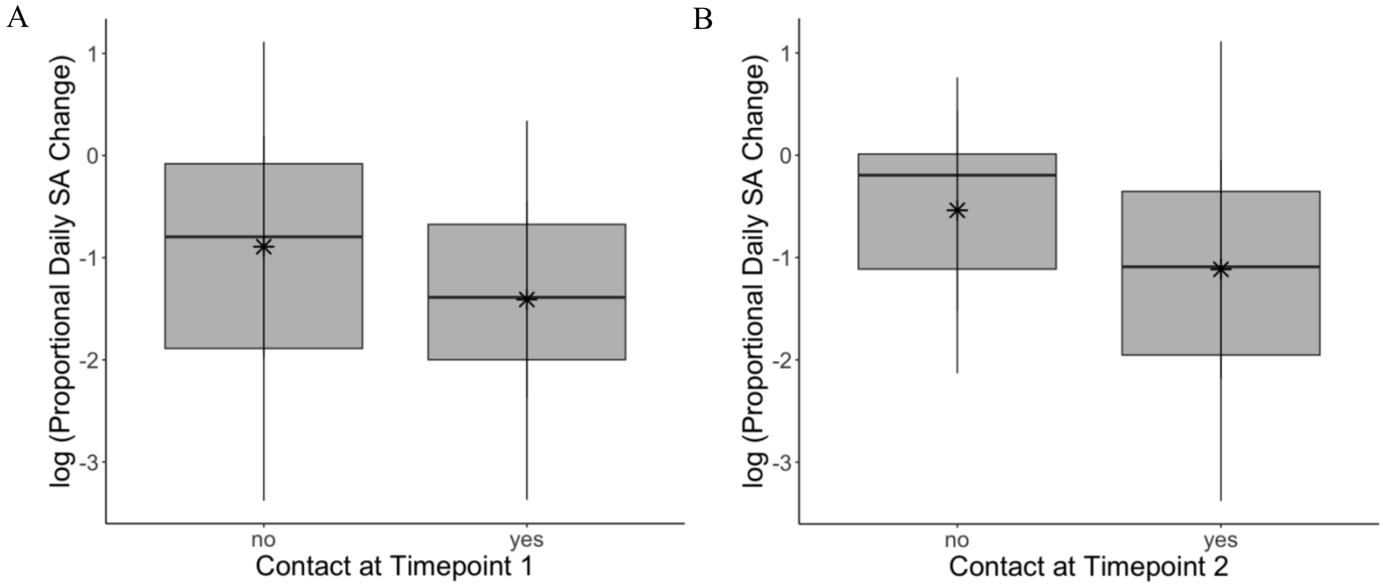

Fig. S8. Boxplots comparing mean log-transformed proportional daily growth rates in surface area (SA) between *M. capitata* corals that were in contact with other colonies (yes) and corals that were not in contact with other colonies (no). Because some corals had no contact with other colonies in 2019 but grew into other colonies by 2021, (A) is for coral contact classified in 2019 and (B) is for coral contact classified in 2021.

In 2019, 66 out of 103 colonies were not in contact with other corals, but by 2021, there were very few corals not in contact with other colonies (only 7 out of 103). When contact was classified in 2019, corals in contact with other colonies increased in SA by an average of 0.36% (+/- 0.34 SD) per day (130% (+/- 130 SD) per year), while corals not in contact with other colonies increased in SA by an average of 0.68% (+/- 0.68 SD) per day (250% (+/- 250 SD) per year). When contact was classified in 2021, corals in contact with other colonies increased in SA by an average of 0.53% (+/- 0.60 SD) per day (200% (+/- 220 SD) per year), while corals that were not in contact with other colonies increased in SA by an average of 0.83% (+/- 0.68 SD) per day (300% (+/- 250 SD) per year). Proportional daily growth in SA was 1.89 fold lower for corals in contact with other colonies than for corals not in contact with other colonies when contact was classified in 2019 (Fig. S8A), and 1.57 fold lower when contact was classified in

2021 (Fig. S8B). The difference in growth rates between *M. capitata* corals in contact with other colonies and corals not in contact with other colonies was significant when contact was classified in 2019 (student's t(100) = 2.396, p = 0.0186, Fig. S8A) but not significant when contact was classified in 2021 (student's t(100) = 1.389, p = 0.168, Fig. S8B). Although the growth rate of corals with contact was lower than that of corals without contact at both timepoints, the small sample size of colonies with no contact in 2021 may have influenced the statistical significance of these results. Considering colony contact as a factor affecting growth rates is important for assessing the growth of corals in natural reef environments where space may be limited, as well as for comparisons of coral growth rates across studies.

Appendix 3: Protocol for Measuring Coral Colonies from 3D Structure-from-Motion Models using Metashape & TagLab

A complete Structure-from-Motion (SfM) photogrammetry model consists of three components: a 3D mesh, an orthomosaic, and a Digital Elevation Model (DEM). Before beginning this protocol, all of these components should be generated and scaled using the computer software Agisoft Metashape™ (version 1.8.4; Agisoft LLC, St. Petersburg, Russia) following the protocol outlined by Burns et al. (2015), Suka et al. (2019), and Roach et al. (2021). Individual coral colonies can then be measured using the image segmentation software TagLab (version 2023.1.23; Pavoni et al. 2022).

Exporting Models from Metashape

Notes:

- Before beginning to use the TagLab software to annotate models, both an orthomosaic and a DEM must be exported from Metashape.
- TagLab only supports files smaller than 32,767 x 32,767 pixels, and the orthomosaic and the DEM must be the same size for successful import.
- This section will outline how to export a model from Metashape in order to meet these requirements for TagLab.

Steps:

1. Create a rectangular selection of the region to be exported from the completed model by selecting "Draw Rectangle" under the drop-down menu to the left of the ruler in the Metashape toolbar. The selection should be made so that the entirety of the rack fits

within the rectangle, but should exclude any extraneous fragments of the area surrounding the rack.

2. After creating the rectangle, denote it as the outer edge of the portion of the model to be exported by right clicking on the rectangle and selecting “Set Boundary Type” and then “Outer Boundary.”
3. To export the orthomosaic, select “Export” from the drop-down menu under “File” in the toolbar.
4. Select “Export Orthomosaic.” Name the file and export it as a JPEG (.jpg).
5. To comply with TagLab’s file size constraints, select the “Max. dimension (pix)” option and set the size to 30,000 pix.
6. Check the box next to “Clip to boundary shapes” and export the file with all other settings remaining as default.
7. Repeat this process for the DEM by again selecting “Export” from the drop-down menu under “File” in the toolbar, and then “Export DEM.”
8. Name the file accordingly and export it as a TIFF (.tif).
9. Again select the “Max. dimension (pix)” option, set the size to 30,000 pix, and check the box next to “Clip to boundary shapes.”
10. Export the file with all other settings remaining as default. Finally, note the pixel size (mm/pix) in the Workspace pane for both the orthomosaic and the DEM, ensuring that they are the same.

<u>*Using TagLab*</u>

Steps:

1. Open the TagLab program by typing the following code in a command prompt window:

“cd Desktop\TagLab-main” (press enter)

“python.exe TagLab.py” (press enter)

2. Create a map that consists of both the orthomosaic and the DEM that were made in and exported from Metashape. Select “Add New Map…” from the Project tab in the top TagLab toolbar.
3. Name the map and specify the file locations for both the orthomosaic and DEM, the date on which the photos for the map were taken (Acquisition Date), and the pixel size of the files (obtained from Metashape). This process can be repeated to create multiple maps in the same project file, such as for successive models of the same rack over time.
4. Once the map(s) are successfully displayed in TagLab, begin measuring corals. The following procedure will be repeated for each coral colony to be measured and identified.

4-Clicks Segmentation Tool

Steps:

5. To start measuring, select the 4-clicks segmentation tool, denoted as the icon in the toolbar on the left side of the window with the number 4 surrounded by four cross cursors.
6. With the tool selected, zoom in on an individual coral colony and identify the four extremes of its perimeter: top, bottom, left, and right.
7. While holding down the shift key, make a single click at each of these extremes. Successful clicks will be marked with red X’s.
8. Once all four extremes have been identified, the program will automatically create an outline around the colony’s perimeter.

9. TagLab can automatically refine an outline with the Refine tool, which can be used by pressing the R key on the keyboard as many times as necessary to most accurately refine the shape's outline.

<u>Positive/Negative Clicks Segmentation Tool</u>

Notes:

- Use the positive/negative clicks segmentation tool to further refine an outline if it includes areas of the orthomosaic that are not part of the coral colony or excludes areas that are.
- This tool is denoted as one open and one closed circle separated by a curving line in the left toolbar.
- To ensure this tool is used correctly, include the entire colony in the frame of view and confirm it is selected by double-clicking the shape, making its outline white.

Steps:

1. Select the tool from the toolbar.
2. Identify areas of the model to be included in the shape by holding the shift key and making left clicks, which appear as green circles.
3. Mark areas of the model to be excluded from the shape by holding the shift key and making right clicks, which appear as red circles.
4. Once sufficient positive and negative clicks are made to define the colony's outline, confirm the operation by pressing the spacebar on the keyboard.

Freehand Segmentation Tool

Notes:

- Additional manual edits to a colony's outline can be made using the freehand segmentation tool, denoted as a pencil icon in the left toolbar.
- This tool is useful for outlining more intricate, complex areas of a colony's skeleton such as branches, cracks, and cavities.

Steps:

1. With a colony selected, hold down the left mouse cursor and draw a line that outlines the parts of the colony to be included in the shape. For this operation to be successful, ensure that the manually-drawn line both starts and ends in connection with the existing shape's outline.
2. Confirm the task by pressing the spacebar.

Classifying Corals

Notes:

- Once the colony's outline is refined to measurement standards, the shape should be labeled with a class, usually denoted as genus or species name.
- The box in the top right of the TagLab window displays the number of objects identified in each class, as well as the percentage of the total area of the map covered by the objects in each class.

Steps:

1. Select a coral outline.
2. Find the colony's class in the box at the top of the toolbar on the right side of the TagLab window.

3. Set the class of the object by double clicking on the class name. The program will shade the shape with the color associated with the selected class.

Measuring Corals

Notes:

- Each colony that has been measured receives an ID number in TagLab, which is displayed in the data table in the right toolbar.
- Clicking on an individual ID displays the properties of the shape in the Region Info box just below the data table, which includes TagLab's measurements of area and perimeter for the shape.

Steps:

1. To calculate surface area for all the outlined shapes, select "Calculate Surface Area" under the DEM tab on the top toolbar. The surface area for each colony is then displayed in addition to the other properties in the Region Info box.

Model and Colony Comparisons

Notes:

- Once all *M. capitata* coral colonies have been outlined on two separate models of the same rack, where each model represents a different point in time, the colony outlines can be matched and compared to one another across time points.

Steps:

1. Select the "Split Screen" icon on the left toolbar to display both orthomosaics next to each other on the same screen.
2. Select the "Add manual matches" icon, also from the left toolbar.

3. With the screen split into two models from two time points of the same rack, select the same coral on both models. Press the spacebar on the keyboard to confirm the operation and save the match. Each match will be displayed in the Comparison Table on the right toolbar, including both colony ID numbers, the area of both shapes, the colonies’ class or taxonomic identification, and whether the colony was born, grew, shrank, died, split, or fused with another colony.