

## **Relative contributions of size and shape to coral demography**

Manuscript type: **Major Articles**

Keywords:

Demography, Morphology, Modular organisms, Population dynamics, Structure-from-Motion

Guanyan Keelung Chen<sup>1,\*</sup>, Lisa C. McManus<sup>1</sup>, Tung-Yung Fan<sup>2</sup> and Joshua S. Madin<sup>1</sup>

1. Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii, United States of America, 96744; 2. Department of Planning and Research, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan, 944401.

\* Corresponding authors; email: [guanyan@hawaii.edu](mailto:guanyan@hawaii.edu)

**ORCIDs:** Chen, <https://orcid.org/0000-0002-7078-1522>; McManus, <https://orcid.org/0000-0002-9367-6872>; Fan, <https://orcid.org/0000-0003-2144-3970>; Madin, <https://orcid.org/0000-0002-5005-6227>.

## Abstract

It has been 40 years since Hughes (1984) put forward that size of modular corals is a better predictor of demographic fates than age. However, colonies of similar size may exhibit different shapes, and shape holds great ecological and evolutionary significance. This study used orthomosaics of coral reefs to track changes of 796 *Pocillopora acuta* colonies in Kenting National Park, Taiwan over two years. We quantified relationships between coral demographic fates and three morphological traits: planar area (size), circularity (shape) and perimeter/area ratio that integrates size and shape. Together, area and circularity consistently explained the most variation for all modular processes except shrinkage, which was explained best by area alone. Including circularity with area significantly improved the capacity to predict survival and fission, with large and circular colonies surviving better, and large and irregular colonies more prone to fission. Circularity also improved predictions of proportional area change, with smaller circular colonies experiencing higher rates of change. Fusion was unrelated to any single morphological trait, presumably because it relies on proximity in space. Perimeter/area ratio is the best single trait for survival prediction. Our results highlight that size and shape should both be considered for the demographic modeling of modular organisms.

## Introduction

A demographic understanding of plant and animal populations—i.e., where populations can grow or become locally extinct—is a cornerstone of ecology and evolution (Keyfitz and Caswell, 2005). For solitary organisms, rates of growth, mortality and reproduction tend to vary mostly with age or life history stage as they grow (Stearns, 1976; Hutchings, 1993). However, modular organisms can both grow and shrink with age as modules are added or subtracted through time. Modular organisms can also break into multiple individuals (fission) and, vice versa, multiple individuals can fuse into one (fusion). Fates of various modular processes significantly alter rates of proportional change in living area and simultaneously affect population density (Hughes et al., 1992; Forsman et al., 2015). Since Hughes and Jackson (1980) suggested that modular corals could “lie about their age,” population models of modular organisms have been almost exclusively parameterized using size.

Indeed, size has been shown to be a good predictor of demography. For example, larger coral colonies typically experience lower mortality (Hughes and Connell, 1987), at least up to a point where they can become mechanically vulnerable (Madin et al., 2014). Size is also associated with strategies for energy investment in growth and fecundity (Bonilla et al., 2023; Soong, 1993). Smaller colonies exhibit higher growth rates (Carlot et al., 2021; Dornelas et al., 2017), while larger colonies can produce more offspring (Hall and Hughes, 1996; Álvarez-Noriega et al. 2016). The size structure of coral populations has therefore been used to assess population health and predict dynamics (Bak and Meesters, 1998). For example, prolonged exposure to high temperatures can reduce the average size of colonies and affect their resilience (Speare et al., 2022). Smaller corals can enhance reef resilience by their rapid growth, but they also exhibit greater vulnerability to disturbances (Carlot et al., 2021). Meanwhile, modular growth can lead to a variety

of shapes for a given size (Figure. 1), which could potentially explain as much, or more, variation in demographic rates than size alone.

The shape of modular organisms is important in modulating demographic rates (Jackson, 1979). For example, a series of studies on 11 coral species showed that relationships between colony size and mortality, growth and reproduction tended to be more similar for species with similar growth forms (Dornelas et al., 2017; Madin et al., 2020). Species with similar morphological traits also tend to have similar life history strategies (Darling et al., 2012) and ecosystem function roles (Madin et al., 2023). Shape also affects demographic processes among species in other modular taxa, such as the filtering efficiency of barrel sponges (McMurray et al., 2014) and survival rates in high-sediment environments (Pineda et al., 2016). Additionally, tunicates exhibit a more flattened shape in environments with strong water movement to increase their survival and reproductive output (Holyoak, 1997).

However, few studies have demonstrated the importance of considering the demographic implications of size and shape within the same species. Previous studies on modular organisms' morphology have primarily focused on the differences among functional groups or species. The descriptions of shape are mostly discrete and non-quantitative, such as categorizing colony shapes into massive, encrusting, or branching (Denis et al., 2017; McWilliams et al., 2022). This discrete classification fails to adequately capture the subtle differences between colonies and makes it difficult to integrate into mathematical models. Colony shapes can exhibit high plasticity, resulting in significant variation even within the same species (Forsman et al., 2009; Muko et al., 2000; Paz-García et al., 2015).

Predicting the proportional change of area, also known as the growth rate, has been the goal of many past studies, as the proportional change of area can approximate critical ecological indicators,

such as productivity and resilience (Anthony et al., 2011; Vile et al., 2006). In addition to growth and shrinkage affecting the proportional change of area, fission and fusion can also lead to changes in growth rate. Nonetheless, previous research has seldom explored the morphological factors that lead to the occurrence of fission and fusion. Fission can increase the number of colonies with the same genotype, reducing the risk of genotype extinction. Fission can also enable a population to propagate more quickly than growth and sexual reproduction alone (Tunncliffe, 1981). By producing relatively larger fragments and bypassing the planula larval and early settlement stages, fission increases survival rates during the juvenile stage (Highsmith, 1982) and also enhances the efficiency of nutrient acquisition (McFadden, 1986). However, fission may reduce fecundity due to a relatively higher investment of energy into tissue repair and growth (Zakai et al., 2000) and increase the risk of spreading diseases through higher rates of direct contact with adjacent colonies (Brandt et al., 2013). Fusion on the other hand accelerates colony growth (Forsman et al., 2015) allowing colonies to escape size-dependent mortality agents, including thermal stress (Huffmyer et al., 2021). Explicitly considering fission and fusion can thus provide a more complete understanding of coral population dynamics.

This study aimed to move beyond an inter-specific understanding of growth form on the demography of modular organisms by tracking the fates of hundreds of morphologically variable colonies of a branching coral species over two years. We linked two-dimensional (2D) morphological traits— size, circularity, and perimeter-to-area (P/A) ratio— with rates of modular processes and proportional area change of coral colonies. Size and circularity are independent measures of morphology, allowing us to partition variation explained by each; we can then compare these models with perimeter/area ratio, which captures size and shape in a single metric. The P/A ratio has been used as an indicator of colony defense capabilities (George et al., 2021)

86 and damage patterns (Meesters et al., 1997), while circularity has been employed to assess its  
87 importance in growth models (Madin et al., 2020) and to evaluate shape differences among various  
88 habitats (Brambilla et al., 2022). Our overarching question is: What are the relative contributions  
89 of size and shape to modular processes and the proportional area change? Our findings will help  
90 determine if shape should be considered in intra-species demographic models.

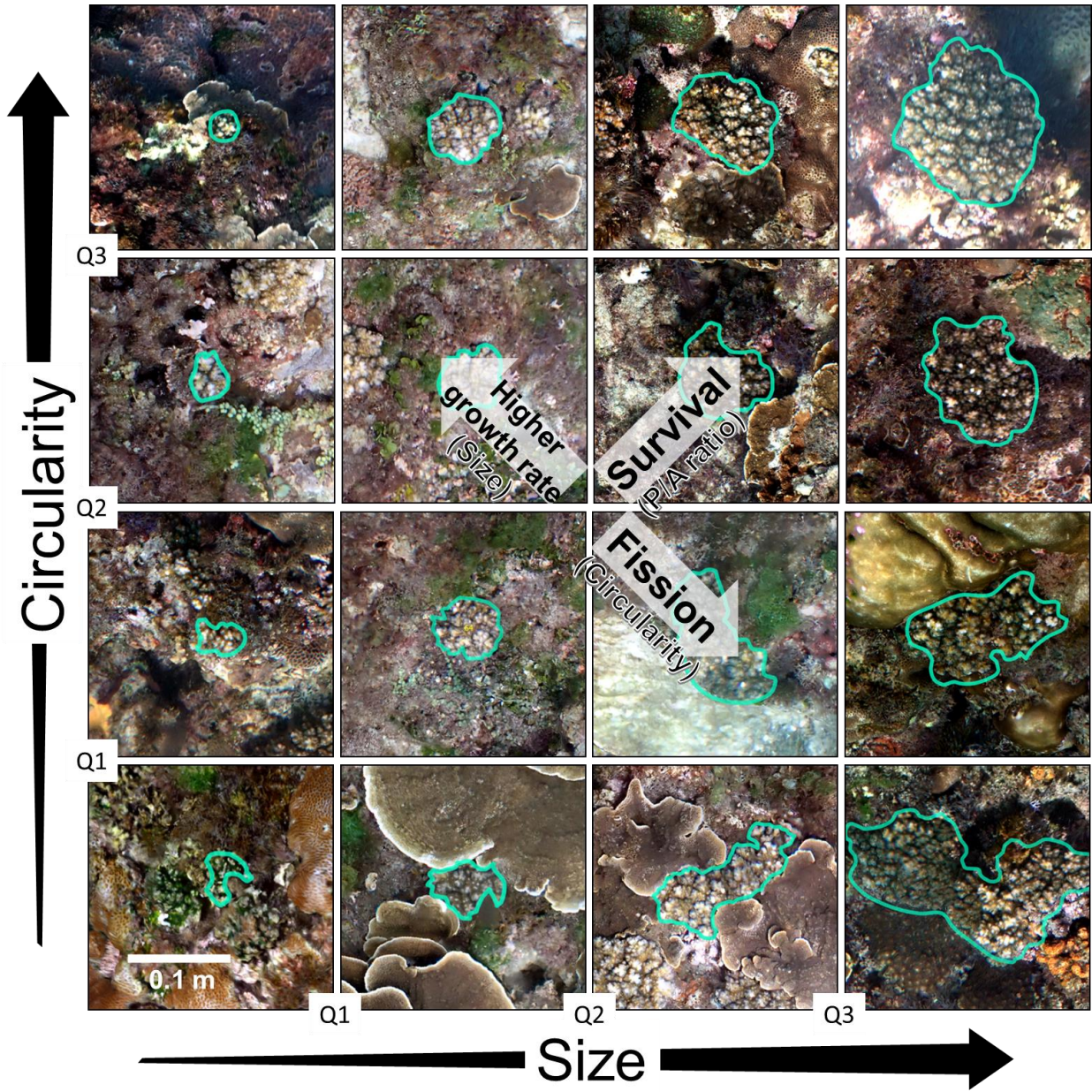


Figure 1: The morphological diversity of *Pocillopora acuta* colonies. The X-axis represents increasing size and the Y-axis represents increasing circularity. Q1 to Q3 represent the quartiles for size and circularity. The example images use colonies delineated in this study, with a scale bar in the lower left corner. The white arrow in the center of the image indicates the demographic fates related to morphology and its highest-ranked explanatory single traits found in this study, with detailed descriptions available in the results section.

## Methods

### *Study site and colony delineation*

This study was conducted in Kenting National Park, Taiwan (21°55'55.94"N 120°44'42.67"E). Three surveys were conducted yearly over a two-year period (Oct 2020 to Dec 2022, the recent disturbance history see Figure S1). During each survey, site images were collected using Structure-from-Motion (SfM) photogrammetry to generate georeferenced high-resolution orthomosaics, therefore facilitating the precise tracking of the fate and morphological changes of coral colonies through time (Couch et al., 2021; Ferrari et al., 2021). The construction of orthomosaics was carried out using Agisoft Metashape Professional (Version 2.0.0 build 15597). We followed the survey and software operation processes described in Burns et al. (2015) and Chen and Dai (2021). We used two parallel Olympus TG-6 cameras set to interval shooting and maintained a distance of 0.9-1.4 meters from the substrate. Each square meter had a coverage rate of more than 9 photos. The protocol within the software is detailed in table S2. The output resolution is approximately 0.1 mm/pix, sufficient to distinguish targeted coral species and subtle changes in morphology.

We focused on the locally abundant branching species *Pocillopora acuta*. ArcGIS Pro (version 3.0.3) was used to delineate coral colonies on the orthomosaics. During each time point, the survey

covered three plots with a total area of 84.39 m<sup>2</sup> (see figure S1). The freehand tool in the ArcGIS Edit function was employed to manually delineate all *P. acuta* colonies and to create polygons. A unique ID was assigned to each existing or newly added colony (i.e., recruit) for tracking changes from year to year. On average, each survey identified 265 colonies, with a total of 796 colonies delineated across the three surveys (T1 = 262, T2 = 264, T3 = 270). The two-dimensional surface area and perimeter of each colony were estimated using the R Package *habtools* (Schiettekatte and Madin, 2024). The calculation errors were estimated by using acrylic plates of known area (see figure S3). The relative error in area measurements was within  $\pm 2\%$ , more than 10-times lower than the mean proportional change of area in coral colonies between surveys.

#### *Modular processes and morphological traits*

The modular processes of coral colonies were categorized as: (1) mortality, (2) growth, (3) shrinkage, (4) fission, and (5) fusion. Mortality was defined as the absence of any living tissue in the same location during the subsequent survey. Growth and shrinkage were determined by the increase or decrease in the area of the same colony between two surveys, respectively. Fission referred to a scenario where a single colony was observed as multiple separate colonies in the next survey. In a rare case ( $N = 1$ ), a newly added colony that was not classified as a recruit due to its size was also categorized as a colony that has moved over long distances due to nearby fission. Fusion occurred when multiple nearby colonies merged into a single entity encompassing all original locations during the next survey, with their living tissue showing no apparent separation or color differences (a diagram about modular processes can be found in figure 2). Note that the total area change resulting from fission and fusion may either increase or decrease (figure S4).

Three morphological traits for each colony—size, perimeter-to-area (P/A) ratio, and circularity—were used to assess their relationship with modular processes. Size is simply the planar area of the



coral colony. The P/A ratio considers both the perimeter and area of the colony, but is more strongly correlated with size ( $R^2 = 0.92$ ); colonies of the same size but with a higher P/A ratio have more irregular shapes. Circularity is a measure of shape of a colony that is independent of size ( $R^2 = 0.09$ ), and is calculated as the ratio of the circumference of a circle with the same area of the colony divided by the perimeter of the colony, given as:

$Circularity = \sqrt{4\pi(Area)} / Perimeter$	(Equation 1)
---	--------------

Circularity is dimensionless and ranges from greater than 0 to 1, with a value of 1 representing a colony that is a perfect circle. To normalize the data distribution of these morphological traits, size and P/A ratio underwent a  $\log_{10}$  transformation, while circularity was subjected to a logistic transformation. The calculations for morphological traits and data transformations were performed using the R package Habtools (Madin & Schiettekatte, 2024).

### *Analysis*

To calculate the probability of different modular processes occurring for various colony morphologies, the occurrence of each fate was converted into binary distribution data composed of 0s and 1s such that 1 represents survival and 0 represents mortality. After excluding colonies that died, we calculated the probability of undergoing growth, shrinkage, fission, or fusion. We also measured proportional change in area based on morphology, which was calculated as the final area divided by the initial area. A proportional change of 0 indicates mortality, a value between 0 and 1 indicates shrinkage, a value equal to 1 indicates no change, and a value greater than 1 indicates growth. Since fission and fusion involve area changes from one to many or many to one, the rate is calculated proportionally to the summed areas of multiple colonies (see figure S5 for detailed calculation). Additionally, because the three plots in the second survey were not

investigated during the same time period, the proportional change was weighted according to the length of time elapsed (see figure S6) and was  $\log_{10}$  transformed for analysis.

Generalized Linear Models (GLM) were used to evaluate which morphological traits better predict the probability of the various fates and the proportional change in colony areas. The fate models used a binomial link function, and the change models used a Gaussian link function. Predictors were the three morphological traits. Size and circularity were independent and could be used in the same models, whereas P/A ratio was analyzed alone. Interactions between size and circularity were also considered, because shape may affect fates and changes differently at different sizes. Because some colonies were measured repeatedly across the two time periods, and may have exhibited non-independent fates, we ran a preliminary analysis with colony ID and survey times included as random effects using generalized linear mixed models (GLMM). This analysis was conducted in R using the lme4 package (Bates et al., 2015). The random effect explained very little variation for most processes, suggesting that the fate of colonies was largely independent from year to year (Table S7), and therefore we focus on the fixed effects model for simplicity. The McFadden pseudo- $R^2$  was used to assess variance explained and the Akaike Information Criterion (AIC) was used to determine model fit.

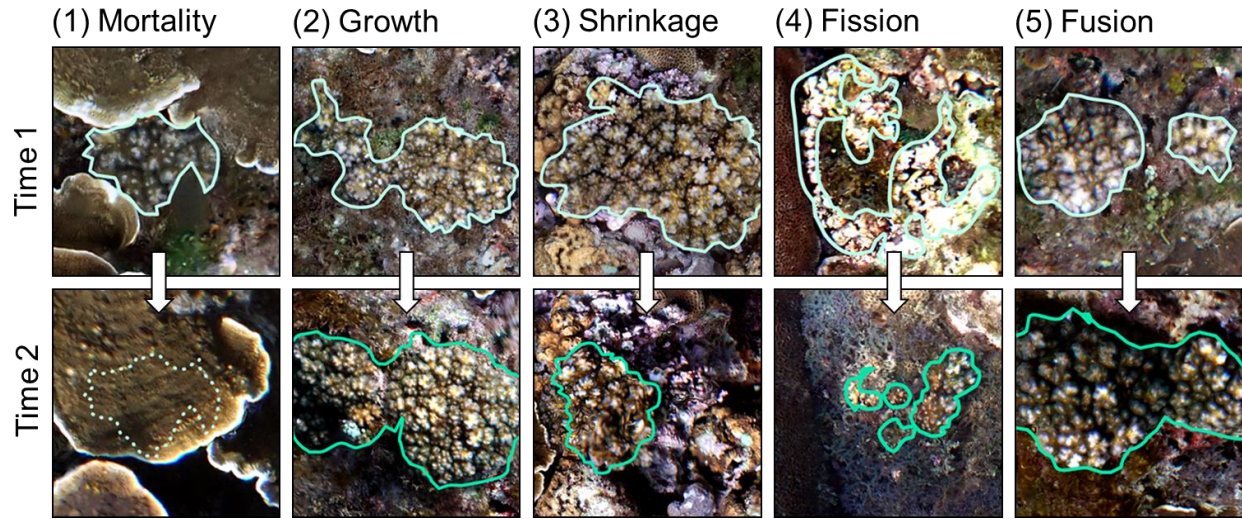


Figure 2: The example diagram of coral modular processes. The areas circled in the diagram showing the before and after changes of the colony following one survey time point.

## Results

When considering morphological traits separately, size explained the most variation in growth and shrinkage, P/A ratio explained the most variation in survival, and circularity explained the most in fission. No variables explained any highly significant levels of variation in fusion (Table 1). However, when size and circularity were considered together, they consistently explained the highest levels of variation for all fates, except for shrinkage, which continued to be strongly controlled by size. Interactions between size and circularity were only found to be highly significant predictors of variations in rates of fusion, suggesting that these traits affect fates independently of each other (Table 1).

Considering both size and circularity together offers the best improvement in predicting survival and fission (Table 1). Size and circularity both positively affected survival. In contrast, for fission, size had a positive effect and circularity had a negative effect (Figure 3). We note that the P/A

ratio is not the same as size and circularity combined. When the effects of size and circularity on survival are in the same direction, the P/A ratio yields a stronger correlation with survival. When the effects of size and circularity on fission are opposite, the P/A ratio is the weakest predictor of fission among the three. The diagonal direction of demographic fates in Figure 1 summarizes these findings: larger and more circular colonies are more likely to survive (as depicted from the bottom left to the top right of Figure 1), while larger and less circular colonies tend to undergo fission (from the top left to the bottom right of Figure 1).

The effect of size on growth and shrinkage shows an inverse relationship, with larger sizes tending towards shrinkage and smaller sizes towards growth (Figure 3). However, circularity does not exhibit an inverse relationship with growth and shrinkage; only colonies with a high degree of circularity tend towards growth, while low-circularity colonies do not show a clear tendency towards shrinkage (Figure 3). This is because once fission and fusion are taken into account, growth and shrinkage are no longer inherently opposing relationships.

Considering both size and circularity together also confers the best prediction for proportional change of area. Among the three traits, size has a notably stronger negative effect on the growth rate, which is opposite to the effect of circularity (Table 2; Figure 4). Specifically, for every tenfold increase in colony area, the expected proportional change decreases by approximately 65%. Due to the opposing effects of size and circularity, with size having a significantly stronger impact, the predictive capability of the P/A ratio falls between the two other predictors (Table 2). Given that the smaller and more circular coral colonies are expected to have higher proportional change of area, this morphotype is also less prone to fission, as indicated by the diagonal line from the bottom right to the top left in Figure 1. Thus, this result further indicates that coral colonies with lower growth rate are more inclined towards fission.

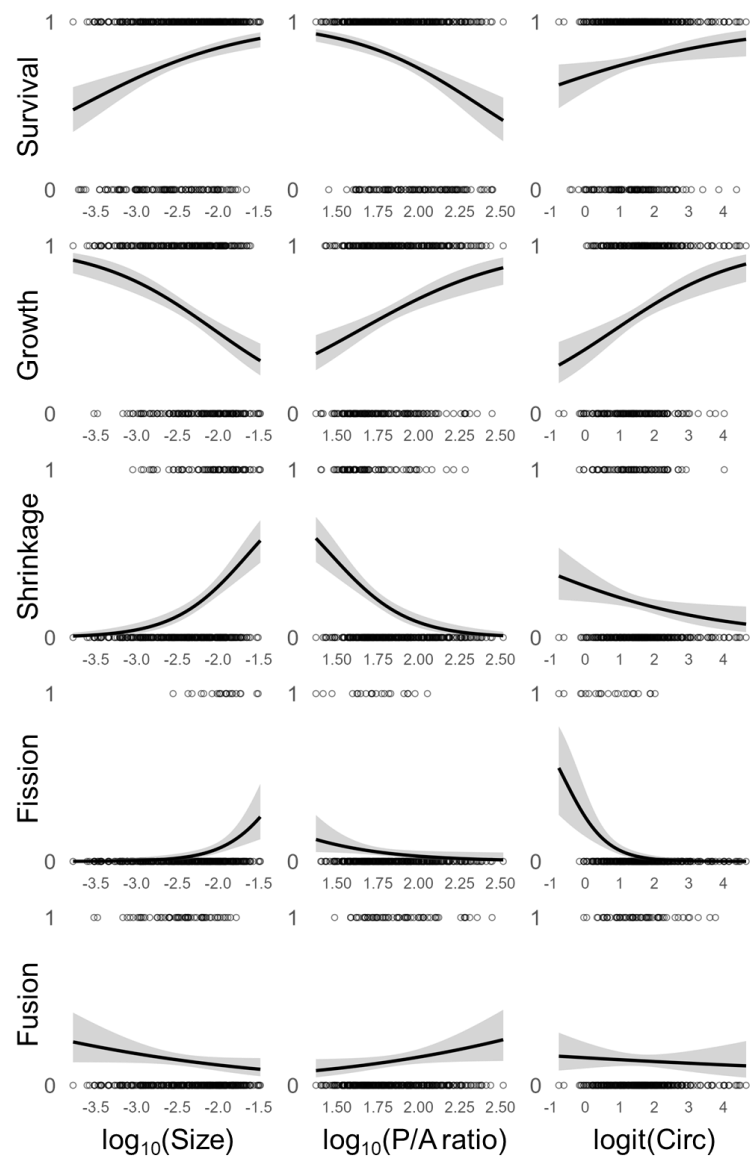
215

216 Table 1: Model selection statistics for morphological trait effects on fates. Bold indicates the model  
 217 with the lowest AIC value. Asterisks indicate the significance level ( $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p$   
 218  $< 0.1$  \*). The numbers in parentheses in the  $R^2$  column represent the difference between the  
 219 combined size/circularity model and the size-only model. Size and P/A ratio were  $\log_{10}$   
 220 transformed, while circularity was logit transformed.

Model	Estimate	d.f.	AIC	$R^2$
Survival ~ Size	1.004 ***	524	550.3	0.04
Survival ~ P/A ratio	-2.547 ***	524	539.7	0.06
Survival ~ Circularity	0.303 *	524	567.4	0.01
<b>Survival ~ Size + Circularity</b>	<b>1.301 *** 0.549 ***</b>	<b>523</b>	<b>534.6</b>	<b>0.07 (+0.03)</b>
Survival ~ Size + Circularity + Size : Circularity	1.134 * 0.838 0.113	522	536.4	0.07
Growth ~ Size	-1.368 ***	402	512.8	0.07
Growth ~ P/A ratio	2.175 ***	402	526.8	0.04
Growth ~ Circularity	0.554 ***	402	527.8	0.04
<b>Growth ~ Size + Circularity</b>	<b>-1.164 *** 0.383 **</b>	<b>401</b>	<b>506.1</b>	<b>0.08 (+0.01)</b>
Growth ~ Size + Circularity + Size : Circularity	-0.775 -0.215 -0.255	400	507.5	0.08
<b>Shrinkage ~ Size</b>	<b>2.204 ***</b>	<b>402</b>	<b>365.0</b>	<b>0.12</b>
Shrinkage ~ P/A ratio	-4.266 ***	402	370.2	0.11
Shrinkage ~ Circularity	-0.350 *	402	408.4	0.01
Shrinkage ~ Size + Circularity	2.182 *** -0.030	401	367.0	0.12 (+0.00)
Shrinkage ~ Size + Circularity + Size : Circularity	2.190 ** -0.041 -0.005	400	369.0	0.12
Fission ~ Size	2.856 ***	402	148.3	0.13
Fission ~ P/A ratio	-2.459 *	402	163.9	0.03
Fission ~ Circ	-1.634 ***	402	141.7	0.17
<b>Fission ~ Size + Circularity</b>	<b>2.125 ** -1.391 ***</b>	<b>401</b>	<b>133.6</b>	<b>0.23 (+0.10)</b>
Fission ~ Size + Circularity + Size : Circularity	1.016 0.543 1.474	400	134.1	0.24

Fusion ~ Size	-0.521	402	336.6	0.01
Fusion ~ P/A ratio	1.187 *	402	336.0	0.01
Fusion ~ Circularity	-0.087	402	339.7	0.00
Fusion ~ Size + Circularity	-0.624 *	401	337.1	0.01 (+0.00)
<b>Fusion ~ Size + Circularity + Size : Circularity</b>	<b>-2.807 ***</b> <b>3.236 **</b> <b>1.392 **</b>	<b>400</b>	<b>328.0</b>	<b>0.05</b>

221



222

Figure 3: The effect of each morphological trait on fate probability. Only pairwise effects are shown, even if non-significant or a significant interaction was found (e.g., as for fusion; Table 1). Circles represent data points. The Y-axis denotes the occurrence of a fate with 1 indicating occurrence and 0 indicating non-occurrence. The shaded band represents the 95% confidence interval. The black solid line represents the fit of the binomial distribution GLM model.

Table 2: Model selection statistics for morphological trait effects on proportional change of area. Bold indicates the model with the lowest AIC. Asterisks indicate the significance level ( $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p < 0.1$  \*). The numbers in parentheses in the  $R^2$  column represent the difference between the additive model and the Size model. The proportional change was  $\log_{10}$  transformed.

Model	Estimate	d.f.	AIC	$R^2$
Proportional change ~ Size	-0.428 ***	402	119.3	0.36
Proportional change ~ P/A ratio	0.793 ***	402	163.9	0.28
Proportional change ~ Circularity	0.121 ***	402	254.3	0.10
<b>Proportional change ~ Size + Circularity</b>	<b>-0.396 ***</b> <b>0.056 ***</b>	<b>401</b>	<b>109.2</b>	<b>0.37 (+0.01)</b>
Proportional change ~ Size + Circularity + Size : Circularity	-0.370 *** 0.017 -0.016	400	110.0	0.37

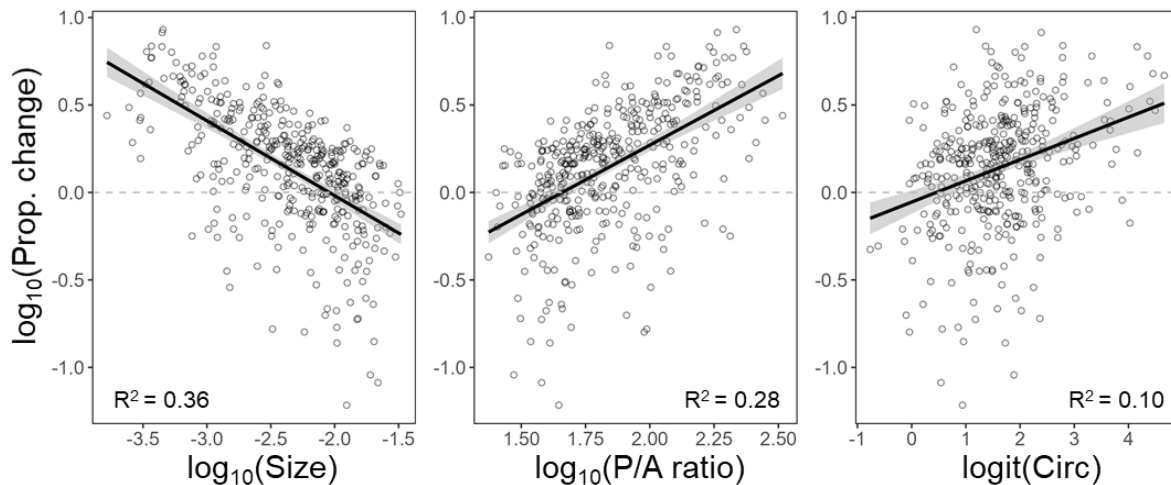


Figure 4: The relationships between three morphological traits and the proportional change of area. Circles representing data points. The gray dashed line indicates a proportional area change of 0, with values above representing growth and values below representing shrinkage. The gray shaded area represents the 95% confidence interval. The black solid line represents the fit of the Gaussian distribution GLM model.

## Discussion

This study demonstrates that intraspecific morphological variability explains significant amounts of demographic variation for a common branching species of reef coral. Indeed, P/A ratio and circularity when considered alone explain more variation in survival and fission than colony size, respectively (Table 1). Moreover, in all cases except shrinkage, considering both size and circularity together improves prediction of modular processes over size alone. Given that modular organisms tend to exhibit high degrees of morphological variation as they grow, such as shown here with *Pocillopora acuta*, our results suggest the addition of measures of individual-level shape (as opposed to species-level categorizations of growth form) in demographic and life history models would result in more robust predictions.

Incorporating shape with size better predicts survival (Figure 3; Table 1) because shape reflects a coral colony's history and its ecological and physiological context. Different environmental conditions (Chappell, 1980; Hossain and Staples, 2020), intense competition (George et al., 2021), limited growth space, past physical damage (Hawkins and Roberts, 1993), or severe partial mortality events, such as predation by coral-eating snails (Hamman, 2018), coral diseases (Aeby et al., 2019), and thermal stress (Speare et al., 2022), can lead to uneven growth in various directions, ultimately resulting in a lower circularity. Conversely, in ideal conditions, undisturbed



coral colonies, such as those restored through suspension methods (Dehnert et al., 2022) or corals cultivated indoors (Leal et al., 2016), tend to grow more rounded due to uniform environmental conditions and fewer disturbances, thus achieving higher circularity. Therefore, it is conceivable that corals with higher circularity in the wild, compared to those with lower circularity, have experienced fewer adverse events, naturally leading to higher survival.

Circularity is the strongest predictor for fission among all coral traits (Figure 3; Table 1). This is likely because circularity can represent the structural integrity of a colony. A circular shape is generally considered capable of evenly dispersing damage, unlike differences in skeletal density among coral species that lead to fission (e.g., branching corals are more prone to fragmentation than massive corals; Chamberlain, 1978). Corals of the same species but with irregular shapes, compared to more rounded colonies, are more likely to experience separation at narrower points due to damage. Additionally, corals naturally grow into irregular shapes that facilitate fission, enhancing asexual reproduction efficiency, such as *Porites* forming ledges at the colony's edge (DeVantier and Endean, 1989). Other colonial organisms like soft corals and tunicates (Ben-Hamo et al., 2022; McFadden, 1986), which rely on tissue extension for fission, also exhibit decreased circularity before fission. Furthermore, as mentioned above, when coral circularity is low, it indicates exposure to adverse events, making the colony more prone to fragmentation due to external forces.

Large and less circular corals tend to exhibit slower growth rates, a phenomenon that past research has confirmed is related to size alone (Dornelas et al., 2017; Hughes and Connell, 1987). By additionally considering circularity, this phenomenon can be better linked to coral life history strategies. Our study found that corals with slower area change rates tend to have a greater propensity for fission (Figure 4; Table 2). This result could suggest an evolutionary adaptation in

coral life history strategies, potentially providing a mechanism for rapidly establishing high-growth colonies independent of sexual reproduction, a trait that might be particularly beneficial in disturbed environments (Hughes and Jackson, 1985; Kayal et al., 2015). As colonies grow larger, their growth rate slows. However, these larger colonies can promote overall population growth by developing irregular shapes that facilitate fission into smaller colonies, which grow more rapidly. This characteristic has also been used as a means to enhance restoration efficiency in corals (Page et al., 2018; Rinkevich, 2000). The process of fragmentation in restoration, akin to natural fission processes, can transform large colonies with slower growth rates into smaller colonies with higher growth rates, achieving a better yield or maintaining better population competitiveness. Therefore, by taking circularity into account as a readily observable indicator, it can help screen colonies suitable for fragmentation restoration or better quantify this strategy of accelerating growth through fission. However, it is important to note that the effects of area change caused by fission may differ for various growth forms of corals. For example, Smith and Hughes (1999) compared the survival rates of staghorn, bushy, and tabular *Acropora* after fragmentation, and only staghorn *Acropora* showed a population growth benefit from fragmentation.

Circularity may have a less pronounced effect on growth or shrinkage compared to size (Figure 3; Table 1). Low-circularity colonies have longer boundaries relative to high-circularity colonies with the same area, indicating more opportunities to access resources for growth (Hoogenboom et al., 2008). However, this also simultaneously increases the possibility of decline due to competition, disease infection, and predation (Meesters et al., 1996; Swierts and Vermeij, 2016; Williams and Miller, 2005). These counteracting effects thus result in the less obvious correlation between circularity and growth or shrinkage. The strong correlation between size and growth or size and shrinkage is likely due to the decrease in nutrient acquisition efficiency as size increases (Marquet

et al., 2005), aligning with past research on allometric growth (Dornelas et al., 2017; Kim and Lasker, 1998). Furthermore, the relationship between circularity and growth or shrinkage does not exhibit as clear an oppositional trend as that shown between size and these processes (with smaller sizes tending towards growth and larger sizes towards shrinkage). Colonies with high circularity tend towards growth, but those with low circularity do not necessarily tend towards shrinkage. This result likely occurs because circularity is more closely related to structural fragility. While our analysis treated fission and shrinkage as independent events, we also found that most fissioned colonies (71%, N=21, Figure S4) experienced a decrease in total area, which may explain why circularity alone is not a strong predictor of colony growth or shrinkage patterns.

Fusion does not show a highly significant correlation with the three morphological traits (Figure 3; Table 1), a likely reason being that fusion is more related to the relative spatial positioning of colonies or historical events that have occurred between them. Fusion is primarily possible between coral colonies that are in close proximity and have genetic relationships (Raymundo and Maypa, 2004). Thus, fusion may be less related to size and shape than other fates. Moreover, fusion tends to occur in colonies that have previously undergone fission (Stocker, 1991), as fission increases the density of colonies within the same area, thereby increasing the likelihood of subsequent fusion. This could also explain why considering the interaction term of size and circularity improves correlation, as colonies that have undergone fission are typically smaller and more irregular. In addition, irregular colonies have longer boundaries, increasing the chance of contact with other colonies, making the interaction term of size and circularity more significant for fusion.

Two-dimensional morphological traits offer the advantages of ease of measurement and high versatility, and they have also demonstrated correlation to demography in this study. They are able

to serve as ‘supertraits’, which capture a large amount of process variation and can accelerate understanding of ecology (Madin et al., 2016). Additionally, 2D traits can be easily quantified from photographs, allowing researchers to leverage historical film and digital collections to create longer demographic time series. However, it is important to note that 2D traits have their limitations in describing morphology. For instance, variations in vertical morphology are not captured by our approach, making it impossible to compare colonies with the same circularity but different growth forms. Also, cryptic species or colonies hidden beneath the reef cannot be adequately quantified in orthographic projection. To enhance the versatility of 2D traits, it is essential first to understand which axis has (horizontal or vertical to the ground) the primary shape variation. Using 2D traits projected along different axes in 3D space for different organisms can better capture intraspecific morphological variations and link them to demography. Future work could determine if 3D traits explain additional variability in demographic processes, and whether 2D and 3D traits are correlated. Recent advances in measurement technologies, such as photogrammetry and 3D scanners, make it easier to obtain quantitative 3D morphological traits, including volume compactness, surface complexity, and top-heaviness. 3D traits such as these have been shown to capture demographic changes caused by ecological disturbances, like bleaching and hurricane events (Zawada et al., 2019b), indicating their potential explanatory power for coral population dynamics.

Although this study focused on intraspecific differences in morphology and conducted model analyses using only one coral species, we expect that different species will exhibit similar morphological change trends when faced with environmental stressors, albeit to a greater or lesser extent depending on species, growth form, and situation. Kaandorp (1999) demonstrated that two distantly related coral genera, *Pocillipora* and *Millipora*, both show a similar trend of

morphological change from thin branching to compact branching with increasing water movement. Doszpot et al. (2019) also noted that *Pocillopora* and *Acropora* exhibit consistent changes in surface complexity along a cross-shelf gradient. McWilliam et al. (2022) further showed that various morphological indicators (surface/volume ratio, corallite size, etc.) of different coral growth forms exhibit similar trends in warmer and more acidic seawater. Additionally, Stocker (1991) found in his study on tunicates that smaller colonies grow faster and elongated forms have higher mortality rates. Despite studying a different modular taxa, the Stocker (1991) results align with the findings of this study. Thus, we suspect that different species will exhibit similar relationships as shown here with *Pocillopora acuta*, but that the degree of occurrence of fates will vary. The associations among colony size, P/A ratio, circularity and modular processes across different species deserves further exploration.

Future work may also consider how historical fates (e.g., what happened in the previous year) will influence current modular processes. For example, Koder et al. (2020) pointed out that colonies that have experienced shrinkage are more likely to shrink again or die in the following year. Recent history may also affect the demographic patterns of different morphology of modular organisms (Tanner et al., 1996). A model that concurrently considers both morphology and the effects of modular processes is likely to have better predictive outcomes. For modular and sessile organisms, the environment significantly shapes their morphology. Colonies that develop morphologies adapted to their environment can achieve higher fitness (Million et al., 2022; Todd, 2008). Fitness of colonies has been explored in past research from various perspectives, including coral genotype (Kenkel and Matz, 2016), symbiotic algae (Muller-Parker et al., 2015), and the composition of symbiotic bacteria (Yang et al., 2017). However, morphology remains the most intuitive and easily measurable indicator, making it a suitable method for preliminary identification of demographic

and environmental conditions. A comprehensive interpretation of morphological variability requires consideration of both size and shape (Zawada et al., 2019a). Previous studies have discussed the relationship between growth forms and fecundity across different species (Álvarez-Noriega et al., 2016), but there is limited research on how morphological changes within the same species affect fecundity. Investigating the influence of size and shape on maturity and fecundity would be a valuable follow-up study.

Our research reveals that incorporating measures of modular shape yields improved explanatory models for growth rate and most demographic fates relative to those using only size. This underscores the potential to expand the toolset available for demographic studies. Since Hughes (1984) observed that colonies of the same age can exhibit different demographic rates due to variations in size, technological advancements have made the collection of quantified morphological data increasingly accessible, enabling the use of shape information. Our findings suggest that even within the same species, colonies of the same size may exhibit different fates due to variations in morphology. Exploring ways to integrate morphological information into integral projection models or matrix population models may lead to enhanced predictions of population dynamics.

### **Acknowledgements**

We are grateful to Zong-Min Ye, Ming-Qi Jiang, Ting-Hui Zheng and Yu-Ting Chiou for help in fieldwork, and to Nina M. D. Schittekatte for assistance with statistical analyses. G.K.C. thanks to the Ministry of Education, Taiwan, for financial support provided through a fellowship for studying abroad. G. K. C. and J. S. M. were supported by NSF grant #1948946. L.C.M was supported by NSF grant #2233983.

394

### **Statement of Authorship**

395

All authors saw and approved for submission the final version of the manuscript, and all persons

396

entitled to authorship have been named. G.K.C., L.C.M., and J.S.M. conceptualized the work and

397

developed the model; G.K.C. and J.S.M. carried out model analysis and wrote the code; G.K.C.

398

and T.Y.F. collected the field data; T.Y.F. provided field survey equipment; G.K.C. wrote the

399

original draft; all authors contributed to writing, review, and editing of the manuscript

400

### **Data and Code Availability**

401

Data and code are available on GitHub (<https://github.com/keelungchen/SizeShapeDemography>)

402

and archived on Zenodo (<https://doi.org/10.5281/zenodo.14615073>; Chen et al. 2025)

## Literature Cited

- Aeby, G. S., B. Ushijima, J. E. Campbell, S. Jones, G. J. Williams, J. L. Meyer, C. Häse, and V. J. Paul. 2019. Pathogenesis of a tissue loss disease affecting multiple species of corals along the florida reef tract. *Frontiers in Marine Science* 6:493086.
- Álvarez-Noriega, M., A. H. Baird, M. Dornelas, J. S. Madin, V. R. Cumbo, and S. R. Connolly. 2016. Fecundity and the demographic strategies of coral morphologies. *Ecology*, 97(12), 3485-3493.
- Anthony, K. R. N., J. A. Maynard, G. Díaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* 17:1798–1808.
- Bak, R. P. M., and E. H. Meesters. 1998. Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* 162:301–306.
- Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.
- Ben-Hamo, O., I. Izhaki, R. Ben-Shlomo, and B. Rinkevich. 2022. Fission in a colonial marine invertebrate signifies unique life history strategies rather than being a demographic trait. *Scientific Reports* 2022 12:1 12:1–11.
- Bonilla, K. G., J. R. Guest, and M. V. Baria-Rodriguez. 2023. Contrasting reproductive strategies between stress-tolerant and competitive coral taxa. *Coral Reefs* 42:717–728.
- Brambilla, V., M. Barbosa, I. Dehnert, J. Madin, D. Maggioni, C. Peddie, and M. Dornelas. 2022. Shaping coral traits: plasticity more than filtering. *Marine Ecology Progress Series* 692:53–65.



424 Brandt, M. E., T. B. Smith, A. M. S. Correa, and R. Vega-Thurber. 2013. Disturbance driven  
 425 colony fragmentation as a driver of a coral disease outbreak. *PLoS One* 8:e57164.

426 Burns, J. H. R., D. Delporte, R. D. Gates, and M. Takabayashi. 2015. Integrating structure-from-  
 427 motion photogrammetry with geospatial software as a novel technique for quantifying 3D  
 428 ecological characteristics of coral reefs. *PeerJ* 2015:e1077.

429 Carlot, J., M. Kayal, H.S. Lenihan, S.J. Brandl, J.M. Casey, M. Adjeroud, U. Cardini, A. Merciere,  
 430 B. Espiau, D.R. Barneche and A. Rovere, 2021. Juvenile corals underpin coral reef carbonate  
 431 production after disturbance. *Global Change Biology*, 27(11), pp.2623-2632.

432 Chamberlain, J. A. 1978. Mechanical properties of coral skeleton: compressive strength and its  
 433 adaptive significance. *Paleobiology* 4:419–435.

434 Chappell, J. 1980. Coral morphology, diversity and reef growth. *Nature* 1980 286:5770 286:249–  
 435 252.

436 Chen, G. K., and C. F. Dai. 2021. Using 3D photogrammetry to quantify the subtle differences of  
 437 coral reefs under the impacts of marine activities. *Marine Pollution Bulletin* 173:113032.

438 Chen, G. K., L. C. McManus, T. Y. Fan, and J. S. Madin. 2025. Data from: Relative contributions  
 439 of size and shape to coral demography. *American Naturalist*, Zenodo Digital Repository,  
 440 <https://doi.org/10.5281/zenodo.14615073>.

441 Couch, C. S., T. A. Oliver, R. Suka, M. Lamirand, M. Asbury, C. Amir, B. Vargas-Ángel, et al.  
 442 2021. Comparing coral colony surveys from in-water observations and structure-from-motion  
 443 imagery shows low methodological bias. *Frontiers in Marine Science* 8:647943.

444 Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. Mcclanahan, and I. M. Côté. 2012. Evaluating  
 445 life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.

446 Dehnert, I., L. Saponari, P. Galli, and S. Montano. 2022. Comparing different farming habitats for  
 447 mid-water rope nurseries to advance coral restoration efforts in the Maldives. *PeerJ* 10:e12874.

448 Denis, V., L. Ribas-Deulofeu, N. Sturaro, C. Y. Kuo, and C. A. Chen. 2017. A functional approach  
 449 to the structural complexity of coral assemblages based on colony morphological features.  
 450 *Scientific Reports* 2017 7:1 7:1–11.

451 DeVantier, L. M., and R. Endean. 1989. Observations of colony fission following ledge formation  
 452 in massive reef corals of the genus *Porites*. *Marine ecology progress series*. Oldendorf 58:191–  
 453 195.

454 Dornelas, M., J. S. Madin, A. H. Baird, and S. R. Connolly. 2017. Allometric growth in reef-  
 455 building corals. *Proceedings of the Royal Society B: Biological Sciences* 284.

456 Doszpot, N. E., M. J. McWilliam, M. S. Pratchett, A. S. Hoey, and W. F. Figueira. 2019. Plasticity  
 457 in three-dimensional geometry of branching corals along a cross-shelf gradient. *Diversity*, 11(3),  
 458 44.

459 Ferrari, R., L. Lachs, D. R. Pygas, A. Humanes, B. Sommer, W. F. Figueira, A. J. Edwards, J. C.  
 460 Bythell, and J. R. Guest. 2021. Photogrammetry as a tool to improve ecosystem restoration.  
 461 *Trends in Ecology and Evolution* 36:1093–1101.

462 Forsman, Z. H., D. J. Barshis, C. L. Hunter, and R. J. Toonen. 2009. Shape-shifting corals:  
 463 molecular markers show morphology is evolutionarily plastic in *Porites*. *BMC evolutionary*  
 464 *biology* 9:1–9.

465 Forsman, Z. H., C. A. Page, R. J. Toonen, and D. Vaughan. 2015. Growing coral larger and faster:  
 466 Micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ* 2015:e1313.

467 George, E. E., J. A. Mullinix, F. Meng, B. A. Bailey, C. Edwards, B. Felts, A. F. Haas, et al. 2021.  
 468 Space-filling and benthic competition on coral reefs. *PeerJ* 9:e11213.

469 Hall, V. R., and T. P. Hughes. 1996. Reproductive strategies of modular organisms: comparative  
 470 studies of reef- building corals. *Ecology* 77:950–963.

471 Hamman, E. A. 2018. Aggregation patterns of two corallivorous snails and consequences for coral  
 472 dynamics. *Coral Reefs* 37:851–860.

473 Hawkins, J. P., and C. M. Roberts. 1993. Effects of recreational scuba diving on coral reefs:  
 474 trampling on reef-flat communities. *Journal of Applied Ecology* 30:25–30.

475 Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Marine ecology progress series*.  
 476 Oldendorf 7:207–226.

477 Holyoak, A. R. 1997. Patterns and consequences of whole colony growth in the compound ascidian  
 478 *Polyclinum planum*. *The Biological Bulletin*, 192(1), 87-97.

479 Hoogenboom, M. O., S. R. Connolly, and K. R. N. Anthony. 2008. Interactions between  
 480 morphological and physiological plasticity optimize energy acquisition in corals. *Ecology*  
 481 89:1144–1154.

482 Hossain, M. M., and A. E. Staples. 2020. Effects of coral colony morphology on turbulent flow  
 483 dynamics. *PLOS ONE* 15:e0225676.

484 Huffmyer, A. S., C. Drury, E. Majerová, J. D. Lemus, and R. D. Gates. 2021. Tissue fusion and  
 485 enhanced genotypic diversity support the survival of *Pocillopora acuta* coral recruits under  
 486 thermal stress. *Coral Reefs* 40:447–458.

487 Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model  
 488 with a reef coral example. *The American Naturalist*, 123(6), 778-795.

489 Hughes, T. P., D. Ayre, and J. H. Connell. 1992. The evolutionary ecology of corals. *Trends in*  
 490 *Ecology & Evolution* 7:292–295.

491 Hughes, T. P., and J. H. Connell. 1987. Population dynamics based on size or age? A reef-coral  
 492 analysis. <https://doi.org/10.1086/284677> 129:818–829.

493 Hughes, T. P., and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic  
 494 consequences of partial mortality, fission, and fusion. *Science* 209:713–715.

495 Hughes, T. P., and J. B. C. Jackson. 1985. Population dynamics and life histories of foliaceous  
 496 corals. *Ecological Monographs* 55:141–166.

497 Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate.  
 498 *Ecology* 74:673–684.

499 Jackson, J.B.C. 1979. Morphological strategies of sessile animals. In: Larwood G, Rosen BR  
 500 (eds) *Biology and systematics of colonial organisms*. Academic Press, New York, pp 499–555.

501 Kaandorp, J. A. 1999. Morphological analysis of growth forms of branching marine sessile  
 502 organisms along environmental gradients. *Marine Biology* 134:295–306.

503 Kayal, M., J. Vercelloni, M. P. Wand, and M. Adjeroud. 2015. Searching for the best bet in life-  
 504 strategy: A quantitative approach to individual performance and population dynamics in reef-  
 505 building corals. *Ecological Complexity* 23:73–84.

506 Kenkel, C. D., and M. V Matz. 2016. Gene expression plasticity as a mechanism of coral  
 507 adaptation to a variable environment. *Nature Ecology & Evolution* 1:0014.

508 Keyfitz, N., and H. Caswell. 2005. *Applied mathematical demography* (Vol. 47). Springer.

509 Kim, K., and H. R. Lasker. 1998. Allometry of resource capture in colonial cnidarians and  
 510 constraints on modular growth. *Functional Ecology* 12:646–654.

511 Kodera, S. M., C. B. Edwards, V. Petrovic, N. E. Pedersen, Y. Eynaud, and S. A. Sandin. 2020.  
 512 Quantifying life history demographics of the scleractinian coral genus *Pocillopora* at Palmyra  
 513 Atoll. *Coral Reefs* 39:1091–1105.

514 Leal, M. C., C. Ferrier-Pagès, D. Petersen, and R. Osinga. 2016. Coral aquaculture: applying  
 515 scientific knowledge to ex situ production. *Reviews in Aquaculture* 8:136–153.

516 Madin, J. S., A. H. Baird, M. L. Baskett, S. R. Connolly, and M. A. Dornelas. 2020. Partitioning  
 517 colony size variation into growth and partial mortality. *Biology Letters* 16.

518 Madin, J. S., A. H. Baird, M. Dornelas, and S. R. Connolly. 2014. Mechanical vulnerability  
 519 explains size-dependent mortality of reef corals. *Ecology Letters* 17:1008–1015.

520 Madin, J. S., M. O. Hoogenboom, S. R. Connolly, E. S. Darling, D. S. Falster, D. Huang, S. A.  
 521 Keith, et al. 2016. A trait-based approach to advance coral reef science. *Trends in ecology &*  
 522 *evolution* 31:419–428.

523 Madin, J. S., M. McWilliam, K. Quigley, L. K. Bay, D. Bellwood, C. Doropoulos, ... and M. J. van  
524 Oppen. 2023. Selecting coral species for reef restoration. *Journal of Applied Ecology*, 60(8),  
525 1537-1544.

526 Marquet, P. A., R. A. Quiñones, S. Abades, F. Labra, M. Tognelli, M. Arim, and M. Rivadeneira.  
527 2005. Scaling and power-laws in ecological systems. *Journal of Experimental Biology*  
528 208:1749–1769.

529 McFadden, C. S. 1986. Colony fission increases particle capture rates of a soft coral: Advantages  
530 of being a small colony. *Journal of Experimental Marine Biology and Ecology* 103:1–20.

531 McMurray, S. E., J. R. Pawlik, and C. M. Finelli. 2014. Trait-mediated ecosystem impacts: how  
532 morphology and size affect pumping rates of the Caribbean giant barrel sponge. *Aquatic*  
533 *Biology*, 23(1), 1-13.

534 Meesters, E. H., W. Pauchli, and R. P. M. Bak. 1997. Predicting regeneration of physical damage  
535 on a reef-building coral by regeneration capacity and lesion shape. *Marine Ecology Progress*  
536 *Series* 146:91–99.

537 Meesters, E. H., I. Wesseling, and R. P. M. Bak. 1996. Partial mortality in three species of reef-  
538 building corals and the relation with colony morphology. *Bulletin of Marine Science* 58:838–  
539 852.

540 Million, W. C., M. Ruggeri, S. O'Donnell, E. Bartels, T. Conn, C. J. Krediet, and C. D. Kenkel.  
541 2022. Evidence for adaptive morphological plasticity in the Caribbean coral, *Acropora*  
542 *cervicornis*. *Proceedings of the National Academy of Sciences of the United States of America*  
543 119:e2203925119.

544 Muko, S., K. Kawasaki, K. Sakai, F. Takasu, and N. Shigesada. 2000. Morphological plasticity in  
 545 the coral *Porites sillimaniani* and its adaptive significance. *Bulletin of Marine Science* 66:225–  
 546 239.

547 Muller-Parker, G., C. F. D’elia, and C. B. Cook. 2015. Interactions between corals and their  
 548 symbiotic algae. *Coral reefs in the Anthropocene* 99–116.

549 Page, C. A., E. M. Muller, and D. E. Vaughan. 2018. Microfragmenting for the successful  
 550 restoration of slow growing massive corals. *Ecological Engineering* 123:86–94.

551 Paz-García, D. A., M. E. Hellberg, F. J. García-de-León, and E. F. Balart. 2015. Switch between  
 552 morphospecies of pocillopora corals. <https://doi.org/10.1086/682363> 186:434–440.

553 Pineda, M. C., A. Duckworth, and N. Webster. 2016. Appearance matters: sedimentation effects  
 554 on different sponge morphologies. *Journal of the Marine Biological Association of the United*  
 555 *Kingdom*, 96(2), 481-492.

556 Raymundo, L. J., and A. P. Maypa. 2004. Getting bigger faster: mediation of size-specific  
 557 mortality via fusion in juvenile coral transplants. *Ecological Applications* 14:281–295.

558 Rinkevich, B. 2000. Steps towards the evaluation of coral reef restoration by using small branch  
 559 fragments. *Marine Biology* 136:807–812.

560 Schiettekatte, N., Madin, J. 2024. habtools: tools and metrics for 3d surfaces and objects. R  
 561 package version 1.0.5, <<https://CRAN.R-project.org/package=habtools>>.

562 Smith, L. D. and T. P. Hughes. 1999. An experimental assessment of survival, re-attachment and  
 563 fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology*, 235(1),  
 564 147-164.

565 Soong, K. 1993. Colony size as a species character in massive reef corals. *Coral Reefs* 12:77–83.

566 Speare, K. E., T. C. Adam, E. M. Winslow, H. S. Lenihan, and D. E. Burkepile. 2022. Size-  
 567 dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef.  
 568 *Global Change Biology* 28:1342–1358.

569 Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *The Quarterly review of biology*  
 570 51:3–47.

571 Stocker, L. J. 1991. Effects of size and shape of colony on rates of fission, fusion, growth and  
 572 mortality in a subtidal invertebrate. *Journal of Experimental Marine Biology and Ecology*  
 573 149:161–175.

574 Swierts, T., and M. J. A. Vermeij. 2016. Competitive interactions between corals and turf algae  
 575 depend on coral colony form. *PeerJ* 2016:e1984.

576 Tanner, J. E., Hughes, T. P., & Connell, J. H. 1996. The role of history in community dynamics: a  
 577 modelling approach. *Ecology*, 77(1), 108-117.

578 Todd, P. A. 2008. Morphological plasticity in scleractinian corals. *Biological Reviews* 83:315–  
 579 337.

580 Tunnicliffe, V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*.  
 581 *Proceedings of the National Academy of Sciences*, 78(4), 2427-2431.

582 Vile, D., B. Shipley, and E. Garnier. 2006. Ecosystem productivity can be predicted from potential  
 583 relative growth rate and species abundance. *Ecology Letters* 9:1061–1067.

584 Williams, D. E., and M. W. Miller. 2005. Coral disease outbreak: pattern, prevalence and  
 585 transmission in *Acropora cervicornis*. *Marine Ecology Progress Series* 301:119–128.



586 Yang, S.-H., C.-H. Tseng, C.-R. Huang, C.-P. Chen, K. Tandon, S. T. M. Lee, P.-W. Chiang, et al.  
 587 2017. Long-term survey is necessary to reveal various shifts of microbial composition in corals.  
 588 *Frontiers in Microbiology* 8:1094.

589 Zakai, D., O. Levy, and N. E. Chadwick-Furman. 2000. Experimental fragmentation reduces  
 590 sexual reproductive output by the reef-building coral *Pocillopora damicornis*. *Coral Reefs*  
 591 19:185–188.

592 Zawada, K. J. A., M. Dornelas, and J. S. Madin. 2019a. Quantifying coral morphology. *Coral*  
 593 *Reefs* 38:1281–1292.

594 Zawada, K. J. A., J. S. Madin, A. H. Baird, T. C. L. Bridge, and M. Dornelas. 2019b.  
 595 Morphological traits can track coral reef responses to the Anthropocene. *Functional Ecology*  
 596 33:962–975.

## **Relative contributions of size and shape to coral demography**

### **Supplementary materials**

Guanyan Keelung Chen<sup>1,\*</sup>, Lisa C. McManus<sup>1</sup>, Tung-Yung Fan<sup>2</sup> and Joshua S. Madin<sup>1</sup>

1. Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii, United States of America, 96744; 2. Department of Planning and Research, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan, 944401.

\* Corresponding authors; email: [guanyan@hawaii.edu](mailto:guanyan@hawaii.edu)

The American Naturalist

Figure S1: The study site (A, B) and the orthomosaics of 3 plots (C, D, E). The disturbance history during the survey period from Oct 2020 to Dec 2022 is outlined as follows: no typhoon impacts on the area, reduced human disturbance due to COVID-19 restrictions on diving activities imposed by the Taiwanese government, and only one bleaching event that occurred in Aug 2020 prior to the survey.



Table S2: Settings used to generate orthomosaic in Agisoft Metashape Professional (v. 2.0.0).

Performing 2D projection area analysis of coral colonies using SfM can lead to errors such as image blur, incorrect projection angles, and scale distortions (Couch et al., 2021; Bayley & Mogg, 2020). To address image blur, we filmed enough photos with sufficient coverage and avoided using data from the edges of orthomosaic with lower photo coverage. Regarding projection angle and scale distortion, we used a level to ensure consistent projection angles for each survey and used scale bars and standard plates to ensure that the measurement errors were 10-times lower than the annual area change rates of the corals (Figure S3).

Process	Settings
Align photos	High accuracy, generic preselection enabled, 50,000 key point limit, 5000 tie point limit, Enable Adaptive camera model fitting, Gradual Selection and remove noisy points (<25% tie points)
Optimize alignment	Use all Fit selected by the software. Enable Estimate tie point covariance
Build dense cloud	High quality, Mild depth filtering, reuse depth map disabled, Enable Point Cloud Confidence, remove noisy points by Filter by Confidence (Min:0, Max:1)
Build mesh	Arbitrary surface type, high face count, interpolation enabled, calculate vertex colors enabled.
Reference	Coordinate system: Local coordinates (m), Set XY-plane on leveled plate (0.12*0.12m) and Z-axis as depth, 4~5 scale bars (0.3m) were used for referencing and error estimation
Build DEM and Orthomosaic	DEM: Source data: mesh, interpolation enabled Orthomosaic: Blending model Mosaic, surface DEM, enable hole filling, enable ghosting filter

Figure S3: Area measurement error assessment. (A) The red line represents the true area of the acrylic standard plate, and 'error' represents the relative error. The calculation method is the measured area minus the true area, divided by the true area. 'N' represents the number of standard plates, and 'Time' indicates the survey times. (B) The appearance of the scale bar and standard acrylic plate, with length of 30 cm and area of 12 by 12 cm

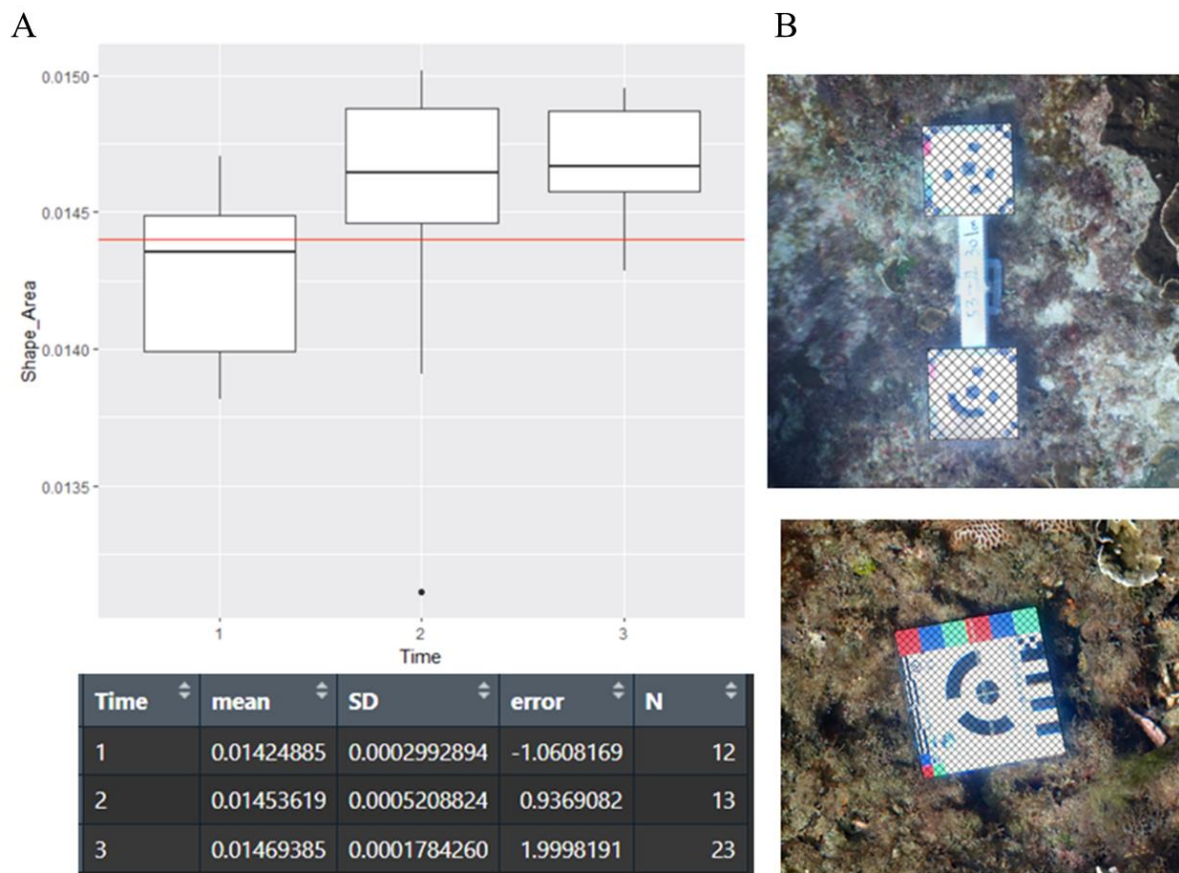


Figure S4: The proportion of total area growth (G) or shrinkage (S) after the fission (Fi, N = 21) and fusion (Fu, N = 59) of coral colonies.

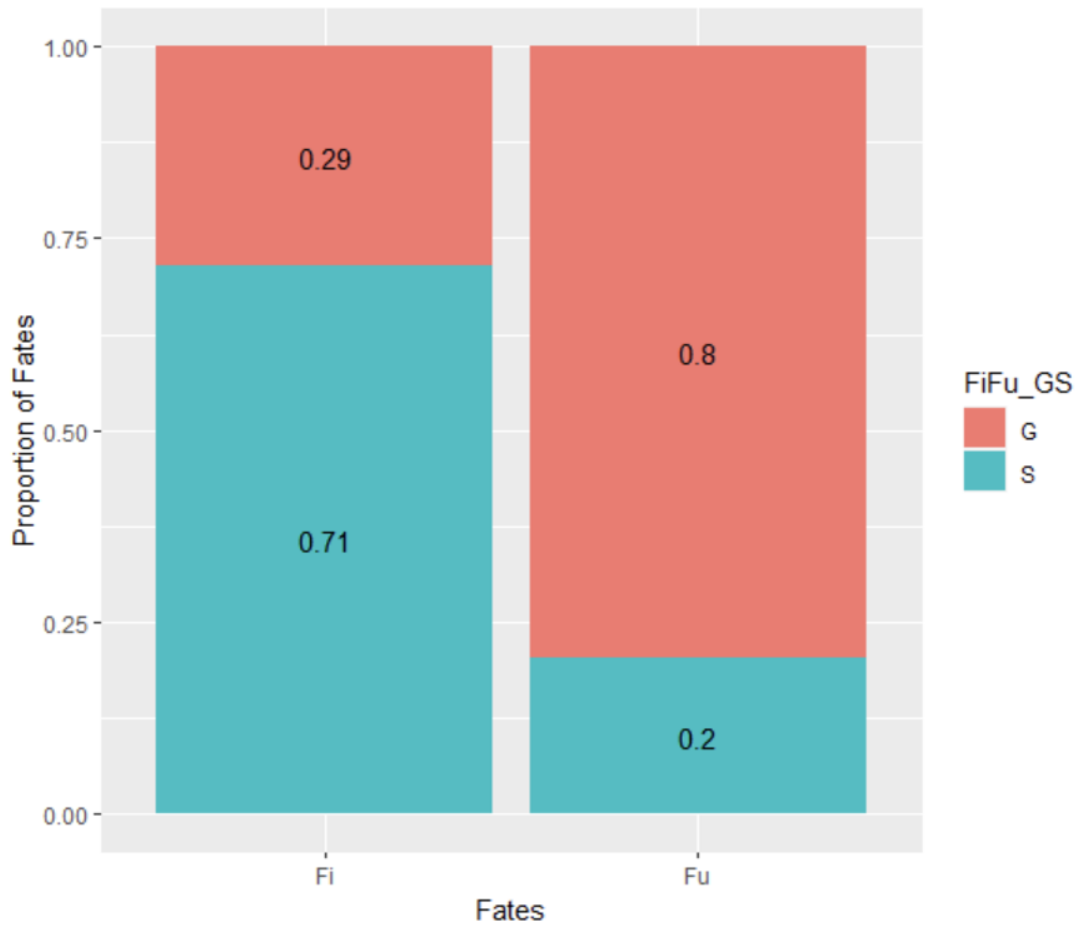




Figure S5: The formula for the proportional area change of coral colonies, with the diagram below illustrating examples of two colonies fusion into one (A1Fu-B, A2Fu-B) and one colony fission into two (AFi-B1B2). "A" represents the area of the coral colony at the original survey time, and "B" represents the area of the colony at the next survey time.

$$\text{Proportional area change} = \begin{cases} \frac{A+(B-A)}{A}, & \text{Growth (G), Shrinkage (S)} \\ \frac{A+(B_1+\dots+B_n-A)}{A}, & \text{Fission (Fi)} \\ \frac{A_i+(B \cdot \frac{A_i}{(A_1+\dots+A_n)} - A_i)}{A_i}, & \text{Fusion (Fu)} \\ 0, & \text{Mortality} \end{cases}$$







Time 1	Time 2	Modular process	Proportional area change of colony at Time 1
		AG-B or AS-B	$\frac{A+(B-A)}{A}$
		A1Fu-B	$\frac{A1+(B \cdot \frac{A1}{A1+A2} - A1)}{A1}$
		A2Fu-B	$\frac{A2+(B \cdot \frac{A2}{A1+A2} - A2)}{A2}$
		AFi-B1B2	$\frac{A+(B1+B2-A)}{A}$

Figure S6: The time intervals between the three surveys. The proportional change of area for coral colonies will be standardized to an annual rate of change (over 12 months) based on the survey time interval.

Plot ID	Survey Time 1 (T1)	Interval T1~T2	Survey Time 2 (T2)	Interval T2~T3	Survey Time 3 (T3)
OL3	10/2020	18	04/2022	8	12/2022
OL2	10/2020	15	01/2022	11	12/2022
OL1	10/2020	17	03/2022	9	12/2022

$$\text{Adjusted proportional change} = \text{proportional change} * \frac{12}{\text{Interval T} \sim \text{T}+1}$$



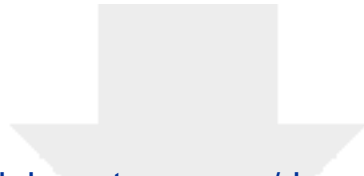
Table S7: The GLMM analysis for random effect of the colony ID and survey times (Time). In the analysis of Survival, Growth, and Shrinkage, IDs were nested within Time to account for non-independent effects among groups. Additionally, due to the change in IDs after fission and fusion, we only analyzed their random effects of Time. The GLM, which excludes random effects, is included in the table as a reference to evaluate whether the model quality improves. If the standard deviation is less than 0.001, it is represented as ~0. Asterisks indicate the significance level ( $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p < 0.1$  \*). This analysis was conducted in R using the lme4 package.

Models	Fixed effects Estimate (GLMM)	Random effect Std. Dev. ID:Time (GLMM)	Random effect Std. Dev. Time (GLMM)	AIC (GLMM )	AIC (GLM)
Survival ~ Size	1.055 ***	0	0.405	544.4	550.3
Survival ~ P/A ratio	-2.636 ***	0.043	0.404	534.2	539.7
Survival ~ Circularity	0.286 *	~0	0.357	563.8	567.4
Survival ~ Size + Circularity	1.345 *** 0.535 ***	0.164	0.388	530.3	534.6
Survival ~ Size + Circularity + Size : Circularity	1.132 * 0.899 0.142	0.135	0.389	532.0	536.4
Growth ~ Size	-1.368 ***	0	0	516.8	512.8
Growth ~ P/A ratio	2.175 ***	0	0	530.8	526.8
Growth ~ Circularity	0.554 ***	~0	0	531.8	527..8
Growth ~ Size + Circularity	-1.169*** 0.384 **	0.139	~0	510.1	506.1
Growth ~ Size + Circularity + Size : Circularity	-0.778 -0.215 -0.255	0.110	0	511.4	507.5
Shrinkage ~ Size	2.204 ***	0	0	369.0	365.0
Shrinkage ~ P/A ratio	-4.266 ***	~0	0	374.2	370.2
Shrinkage ~ Circularity	-0.369	0.577	0	412.4	408.4
Shrinkage ~ Size + Circularity	2.182 *** -0.030	0	0	371.0	367.0
Shrinkage ~ Size + Circularity + Size : Circularity	2.189 ** -0.041 -0.005	0	0	373.0	369.0
Fission ~ Size	2.856***		0	150.3	148.3
Fission ~ P/A ratio	-2.459*		0	165.9	163.9
Fission ~ Circ	-1.634 ***		0	143.7	141.7
Fission ~ Size + Circularity	2.125 ** -1.391 ***		0	135.6	133.6

Fission ~ Size +	1.016			
Circularity +	1.543	0	136.1	134.1
Size : Circularity	1.474			
Fusion ~ Size	-0.521	0	338.6	336.6
Fusion ~ P/A ratio	1.187 *	0	338.0	336.0
Fusion ~ Circularity	-0.087	0	341.6	339.7
Fusion ~ Size +	-0.624 *			
Circularity	-0.193	0	339.3	337.1
Fusion ~ Size +	-2.807 ***			
Circularity +	3.236 **	0	330.0	328.0
Size : Circularity	1.392 **			

### Literature Cited

- Bayley, D. T., & Mogg, A. O. 2020. A protocol for the large-scale analysis of reefs using Structure from Motion photogrammetry. *Methods in Ecology and Evolution*, 11(11), 1410-1420.
- Couch, C. S., Oliver, T. A., Suka, R., Lamirand, M., Asbury, M., Amir, C., ... & Samson, J. 2021. Comparing coral colony surveys from in-water observations and structure-from-motion imagery shows low methodological bias. *Frontiers in Marine Science*, 8, 647943.



[Click here to access/download](#)

**Zip File (for data/code files, will stay zipped)**  
**SizeShapeDemography-v1.0.zip**

