

Coral reef assessments based on cover alone mask active dynamics of coral communities

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ABSTRACT: Coral reef communities are often studied by tracking the percentage (or fraction) of the reef covered by coral through time. However, coral community dynamics result, in part, from underlying colony-level growth and mortality, which in turn depend on characteristics of individual colonies, such as size, taxon, life history strategy, and morphology. Colonies are also subject to external disturbances that propel fission into smaller coral fragments and fusion where related fragments later fuse into contiguous colonies. To quantify how changes in coral growth through time depend on individual colony characteristics and colony fission and fusion processes, 4385 individual Caribbean coral colonies representing 4 dominant coral types (*Madracis mirabilis*, mounding coral species, *Agaricia agaricites*, and *Millepora* spp.) were tracked at 6 mo intervals for 4 yr. Despite overall stable percent coral cover, colonies belonging to different coral types experienced differential growth, shrinkage, mortality, fission, and fusion processes. All coral types displayed size-dependent allometric growth patterns whereby relative, or proportional, growth in colony area decreased with increasing colony size. The largest changes in relative colony growth resulted from colony fission or fusion with other colonies, which occurred in 16.4% of all monitored colonies. Colony longevity, or survival, increased significantly with increasing colony size for all hard-coral groups that did not experience fission, fusion, or a combination of these processes. Our findings illustrate the usefulness of a size- and life-history-dependent approach to coral demography that elucidates the factors driving community dynamics of colonial organisms, which are not captured by traditional approaches based on benthic cover alone.

KEY WORDS: Coral demography · Size dependence · Fission-fusion · Community dynamics · Life history strategy · Morphology

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1. INTRODUCTION

Coral communities are complex mosaics of sexually and asexually produced colonies that differ in terms of size, taxonomy, morphology, and life history strategy—all of which influence coral growth and mortality (Hughes & Jackson 1980, Tanner 2001,

Elahi & Edmunds 2007). Changes in coral reef communities often are studied by tracking the percentage (or fraction) of benthic community covered by coral through time. Such quantifications of changes in total coral cover through time are certainly useful, but miss the underlying dynamics of reef-building constituents, i.e. individual coral colonies (Hughes &

Jackson 1985). For example, individual colonies can grow, shrink, or die, and as such, losses in coral surface of certain colonies can be compensated by increases in coral surface of other colonies. Under balanced scenarios of overall growth and loss, total coral cover through time would remain stable, often taken as evidence that the coral community and population structure under study have not changed between survey periods. However, previous studies emphasizing coral size-based dynamics have detailed various important ecological aspects of coral colony dynamics, including variation in life history strategies, size and morphology, the impact of storms and diseases, etc. (Jackson 1979, Hughes 1996, Vermeij 2006, Hernández-Pacheco et al. 2011, Madin et al. 2014, Riegl & Purkis 2015). Therefore, going beyond percent cover and investigating coral colony characteristics and the demographic processes that drive growth and mortality in individual coral colonies not only builds upon robust size-based ecological approaches to studying sessile communities, but also contributes to a better understanding of the dynamics governing these communities (e.g. Wells 1957, Hughes 1984, Guzner et al. 2007, Edmunds 2010, Vardi et al. 2012, Bernal-Sotelo et al. 2019).

Coral colonies are clonal, or modular, organisms that exhibit relatively indeterminate growth often thought to be limited mainly by external factors (Bak 1976, Buddemeier & Kinzie 1976, Jackson & Coates 1986). Relative or proportional colony growth (new area per unit of existing area), however, often decelerates with increasing colony size for many colonial marine species irrespective of differences in species-specific growth rates (Jackson 1979, Sipkema et al. 2006, Osinga et al. 2011, Pratchett et al. 2015, Dornelas et al. 2017). Intrinsic allometric constraints stemming from the partitioning of resources among growth, reproduction, and maintenance likely underlie the decreasing relative rate of colony growth with increasing colony size (Hughes & Jackson 1985, Osinga et al. 2011, Kayal et al. 2015, Pratchett et al. 2015, Dornelas et al. 2017). For example, differential access to resources across a colony, as with polyps located on a part of a colony unable to access resources, e.g. light or planktonic food resources, requires redirection of available energy from growth and reproduction into overall maintenance of those polyps (Barnes 1973, Kim & Lasker 1998, Anthony et al. 2002). Geometry-based limitations can also influence relative coral growth as the ratio of the colony's perimeter-to-surface area decreases with increasing colony size, i.e. the amount of relative area grown per unit perimeter decreases (Fig. A1 in the Appendix;

see also Pratchett et al. 2015). Growing colonies can also reach a 'critical' size limit when the rate of calcification equals the rate of tissue production (i.e. the point at which the rate of skeletal accretion cannot keep up with tissue growth), a limitation that colonies can accommodate by either increasing skeletal growth, decreasing tissue growth, or changing growth forms (Barnes 1973). All of these behaviors can affect the relative growth rate of an individual coral colony and are also relevant for other benthic invertebrates with similar life history characteristics, such as ascidians, sponges, bryozoans, and gorgonians (Jackson & Winston 1980, Karlson 1988, Lasker 1990, Sipkema et al. 2006, Shenkar et al. 2008, Hart & Keough 2009).

In addition to the effects of colony size and form, colony growth will depend on a species' life history strategy. Life history strategies are consistent, context-independent characteristics of organisms that maximize fitness by differentially allocating resources among growth, reproduction, and survival (Stearns 1992, Darling et al. 2012). Coarsely, life history strategies in corals span a gradient from fast-growing, fast-reproducing species ('*r*-selected') to slow-growing, long-lived, and robust species ('*K*-selected') (MacArthur & Wilson 1967, Buddemeier & Kinzie 1976). Darling et al. (2012) proposed a classification of 4 main life history strategies for scleractinian corals: (1) competitive: fast-growing (*r*-selected) opportunistic species capable of efficient resource uptake, but susceptible to fragmentation during environmental disturbances (e.g. *Acropora* spp.), (2) weedy: fast-growing opportunistic colonizers with intermediate survival probabilities (e.g. *Madracis mirabilis*), (3) stress-tolerant: slow-growing, long-lived (*K*-selected) species, resistant to environmental disturbance (e.g. *Orbicella* spp.), and (4) generalists: species exhibiting moderate growth rates (e.g. *Dichocoenia* spp.). Based on these characterizations, fast-growing weedy corals are expected to exhibit more dynamic changes in colony size through time compared to large, slow-growing, stress-tolerant species, whereas the latter are expected to exhibit higher survival (longevity) because large colonies that dominate populations of these species are less susceptible to total colony mortality (Babcock 1991, Hughes et al. 1992).

The fate of individual coral colonies is also dependent on external factors. A wide variety of disturbances, from hurricane impacts and increasing sea surface temperatures to local increases in sedimentation, can result in whole-colony mortality, partial mortality, temporary coverage/disappearance through burial or bleaching, and colony fission, whereby a larger colony splits into smaller previously connected patches of liv-

ing tissue (Hughes & Jackson 1985, Fong & Glynn 1998, Nyström et al. 2000, Hernández-Pacheco et al. 2011). When recovering from disturbances, colonies can regrow over exposed skeleton, re-emerge from holes, and, because of their clonal nature, fuse with other colonies produced by the original parental colony (Bak 1976, Hughes & Jackson 1980, Tanner 2000, Kayal et al. 2015, Furby et al. 2017).

The relationship between important demographic metrics like colony growth and survival and the range of factors described above, from size-based geometric constraints to life history strategies to dynamical fates (e.g. fission and fusion), are commonly assumed, but nowadays rarely tested and quantified in colonial benthic invertebrates. In this 4 yr study, we focus on the dynamics of individual coral colonies belonging to 4 coral groups representing different life history strategies and morphologies: (1) weedy and branching: *Madracis mirabilis* (Wells 1973), (2) stress-tolerant: mounding coral species, (3) weedy and foliose: *Agaricia agaricites* (Linnaeus 1758), and (4) competitive and foliose: *Millepora* spp. We quantified how colonies changed through time and assessed the influences of colony size, morphology, life history strategy, and fate (e.g. fission and fusion) using log-linear relationships and size-based analyses. The degree to which such mechanisms affect local persistence of coral groups is discussed, as well as how expanding from the predominant focus of studying changes in overall coral cover to include dynamics at the level of individual colonies enriches our mechanistic understanding of coral reefs.

2. MATERIALS AND METHODS

2.1. Study site

Individual coral colonies were tracked for 4 yr from April 2009 to March 2013 on a shallow fringing reef at 6–8 m depth near Westpunt, Curaçao (12° 22' 38" N, 69° 9' 39" W). This site harbors low coral cover communities, interspersed by rubble fields. The corals *Madracis mirabilis*, *Agaricia agaricites*, *Orbicella* spp., and hydrocorals (*Millepora* spp.) have historically dominated the coral communities at this location (Bak 1976, van Duyl 1985). The site is located about 40 km downstream of the urban center of Curaçao and has been known to experience episodic, short-lived storms and ephemeral *Dictyota* spp. algal blooms over the last few decades (de Bakker et al. 2017, S. A. Sandin & M. J. A. Vermeij pers. obs.).

2.2. Focal groups

Based on the corals present at the site, we focused on coral groups representing different combinations of morphologies and life history strategies. We tracked individual colonies belonging to these groups through time using time series of digital imagery.

The 4 coral groups included (1) weedy and branching: *Madracis mirabilis*, (2) stress-tolerant: mounding coral species, (3) weedy and foliose: *A. agaricites*, and (4) competitive and foliose: *Millepora* spp., all of which were classified according to species, except for the mounding group, which included several coral species. *Madracis mirabilis* is a fast-growing, largely heterotrophic species that forms colonies representing densely packed hemispherical clumps of small pencil-sized branches physically connected by a common skeleton, but not always by tissue (Humann & Deloach 2001, Houlbrèque & Ferrier Pagès 2009). Their branching morphology facilitates asexual reproduction through fragmentation, making them a weedy life history species capable of rapidly colonizing large areas (Highsmith 1982, Nagelkerken et al. 2000). The mounding coral group includes the long-lived stress-tolerant life history taxa classically defined morphologically as massive or submassive (i.e. *Orbicella* spp., *Siderastrea* spp., *Diploria* spp., and *Porites astreoides*). This group also included the smaller but arguably still submassive species *A. humilis* (Murdoch 2007). Few colonies of *A. humilis* were included in the data, and results were comparable when omitting this taxon. The foliaceous plating coral *A. agaricites* is an opportunistic (weedy life history) species characterized by high rates of recruitment, growth, and mortality (Hughes & Jackson 1985). *Millepora* spp. are calcareous foliose hydrocorals with a competitive life history strategy (Dubé 2016). They are functionally similar to hermatypic corals in the sense that they contribute to reef construction and can reproduce asexually through fragmentation (Edmunds 1999).

2.3. Survey method and image analysis

We collected a time series of photographs from permanent quadrats within five 400 m² circular plots (11.3 m radius) sited haphazardly parallel to shore and separated from one another by 10–30 m. In each plot, a total of 40 permanent quadrats (60 × 90 cm) were installed and marked with 2 stainless steel eye-bolts and numbered cattle tags. Half of the quadrats (20 per plot) were randomly placed across the plot

(using random number selection of area-weighted polar coordinates); the other half of the quadrats were selected to target colonies of rarer coral taxa. The most abundant coral of this shallow fringing reef is *Madracis mirabilis*, and as such, this species was well-represented in the random quadrats. Efforts were taken to achieve higher sample sizes of the other coral groups (i.e. mounding corals, *A. agaricites*, and *Millepora* spp.) by siting the non-random quadrats around colonies from each of these 3 groups. Notably, this selection protocol included >50% of the small- to medium-sized coral colonies (<1000 cm²) within each of the 3 less-abundant coral groups (i.e. all but *Madracis mirabilis*). This study design, while not purely random, aimed to provide somewhat balanced representation of sample sizes across coral groups. Advances in large-area imaging (e.g. photomosaics) and downstream ecological data analysis can provide facility for *in silico* randomization protocols and would be preferred now that supporting computational capacity is efficient and cost-effective (Edwards et al. 2017, Pedersen et al. 2019). On average, photoquadrats were visited every 6 mo (i.e. every 4–7 mo), at which point a PVC frame was laid on top of the steel eyebolts and photographed using a Canon G12 camera.

Photoquadrats were analyzed using the free program 'photoQuad' (Trygonis & Sini 2012). Each photoquadrat and organisms therein were given a scale based upon calibration from known dimensions of the PVC frame. At each timepoint, all colonies visible in the photoquadrats were manually traced and digitally tagged using a comprehensive naming scheme (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m630p055_supp1.pdf) that permitted tracking colonies in pictures taken at later timepoints to quantify survival and occurrence of fusion, fission, and growth through time. We then analyzed the data generated by photoQuad using MATLAB 7.10.0 (2010a, Statistics & Machine Learning Toolbox).

2.4. Data and statistical analyses

All coral colony measurements were based on 2-dimensional planar projections of colony surface area. Coral growth was defined as proportional change in planar area using the difference of $\log_e(\text{area})$ between subsequent timepoint pairs. This metric provides a way to gauge the relationship between relative areal growth and colony size. Colonies whose surface was covered by the PVC frame within the image at a particular timepoint were not included in the analyses.

Overall, a total of 4385 independent colonies, including 1527 *Madracis mirabilis*, 1209 mounding corals, 578 *A. agaricites*, and 1071 *Millepora* spp., were tracked over the 4 yr of the study period.

2.4.1. Quantifying coral colony dynamics embedded within total coral cover

Elucidating coral colony-level demographic processes allows for a more mechanistic understanding of the dynamics occurring within coral communities, even for sites with stable percent cover. Patterns of decreases and increases in percent coral cover directly resulting from various coral colony demographic processes have been previously described (Furby et al. 2017). We built upon that work by identifying 10 different demographic processes experienced by individual coral colonies at this site from one timepoint to the next. Demographic processes that contributed to increases in coral cover included: (1) recruitment of new colonies from planktonic larval propagules (<1 cm²) (Highsmith 1982, Vermeij 2006), (2) arrival of new fragmented colonies (≥ 1 cm²) transported from outside the quadrats (Bak & Engel 1979, Highsmith 1982, Bruno 1998, Nagelkerken et al. 2000, Vermeij & Bak 2003), (3) re-emergence of colonies previously observed earlier in the time series that had become covered/disappeared due to e.g. sedimentation/algae burial, and (4) colony growth. Demographic processes that contributed to decreases in coral cover included: (5) colony shrinkage and partial mortality, (6) total colony mortality, and (7) covered/disappearance of colonies observed earlier and later in the time series due to e.g. sedimentation/algae burial. Lastly, demographic processes that could lead to either increases or decreases in coral cover included: (8) fission of a parent colony into independent fragments or sub-colonies, (9) fusion of colonies into a continuous colony, and (10) multi-fate dynamics, where sub-colonies experienced multiple demographic processes from one timepoint to the next (Fig. 1). For colonies in the multi-fate category, we calculated colony growth based on the proportional difference in total area of all related sub-colonies at each timepoint.

The reason that fission, fusion, and multi-fate demographic processes result in either an increase or decrease in total coral cover is that colonies can undergo individual growing or shrinking in between time-steps. For example, if a colony with area A_t at time t undergoes fission into 2 sub-colonies with a cumulative area A_{t+1} at time $t + 1$, the change in relative area would either be positive or negative de-

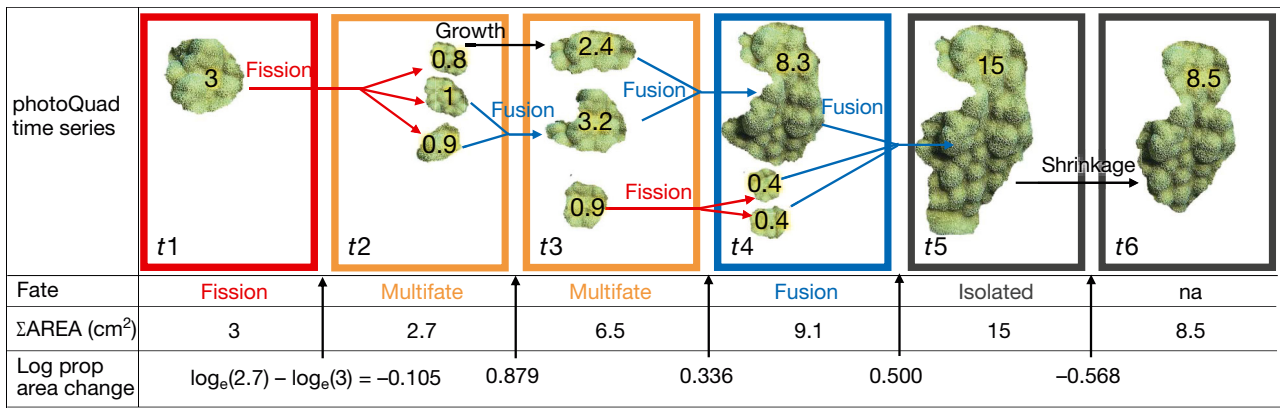


Fig. 1. Hypothetical coral colony growth (same parent colony) through time, and the resulting fate category assignments (red: fission; orange: multi-fate; blue: fusion; gray: isolated). Values superimposed on coral segments represent hypothetical areas. Beneath each quadrat are the sum area of all related colonies per timepoint and the \log_e of proportional change calculation per timepoint pairs. na: not applicable

pending on whether the independent sub-colonies both grew or shrank to a larger or smaller cumulative size than the original parent colony during that time-step. There was also the possibility for zero change if growth in one sub-colony balanced shrinkage in another.

2.4.2. Proportional change in colony surface area

This study quantified colony growth based on proportional changes in colony size, i.e. the difference of the natural log of colony area between 2 timepoints. Because we focused on relative (proportional) colony growth, the relationship between proportional colony growth and initial colony size (on a \log_{10} scale) was plotted for each of the 4 coral groups. To address the generally heteroscedastic and non-linear relationships that emerged (see Fig. 3), a size-class-based analysis was preferred over linear analyses. Choice of size categories was made to use general size ranges common in the literature (e.g. Bak & Meesters 1998, Hughes & Tanner 2000, Meesters et al. 2001, Vermeij 2006) that split the sample size fairly evenly for each taxonomic group (Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m630p055_supp2.xlsx). We divided colonies of each coral group into 3 logarithmically scaled size categories (<1, 1–10, and >10 cm², mapping approximately onto operational definitions of coral ‘recruits’, ‘juveniles’, and ‘adults’, respectively), after which differences in average colony growth could be compared among size classes, coral groups, and 4 main demographical ‘fate’ categories, i.e. isolated colony growth or shrinkage (‘iso’), fission (‘fis’), fusion (‘fus’), or multi-fate (‘mul’). We tested for

significant differences ($\alpha = 0.05$) between the mean proportional change value of the ‘iso’ fate colonies and each of the other fate types by using randomization techniques. The significant relationship between fate and log of proportional change was determined by creating a null distribution of mean proportional change values with randomized fate labels (i.e. resampling without replacement across fates) using 10 000 resampling iterations per size class in each coral group. If observed mean proportional change value by fate was extreme relative to the randomized null distribution, the colony growth by fate was deemed statistically significant.

2.4.3. Longevity patterns

Longevity was defined in this study as the number of timepoints a colony survived during the duration of the study and was quantified only for all coral colonies observed from the first timepoint (April 2009; 2036 total colonies). Adapting the maximum likelihood approach of Vermeij & Sandin (2008), longevity patterns for each of the 4 coral groups were analyzed as a function of colony size class. This was done specifically for both the ‘iso’ (colony growth or shrinkage) fate category and a combined ‘fis/fus/mul’ category, because we were not only interested in distinguishing whether size-based longevity relationships emerged but also in determining whether ‘fis/fus/mul’ fates changed those relationships. Colony size classes were determined based on \log_2 bins (i.e. 0.06, 0.13, 0.25, ..., and 1024 cm²) to increase resolution across the range of colony sizes observed at the beginning of our surveys. Statistical differences

were determined using maximum likelihood estimates of log-linear relationships between mortality (the inverse of longevity) and colony size. Specifically, mortality was modeled after a Poisson distribution capturing the probability of a colony in each size class dying at a given time interval, with rate parameter λ_c , i.e. the mean time until mortality occurs for a colony in size class c . For each coral group \times fate combination, the rate parameter of the Poisson mortality model was constructed in 2 functional forms: (1) assuming a constant uniform mortality probability with size, so $\lambda_c = m_0$, and (2) assuming a log-linear mortality probability with size, so $\lambda_c = m_0 + m_1 \ln(c)$, with the constraint that $\lambda_c > 0$ for all c . The summed log likelihood, L_x , of a particular model describing the observed data given values of mortality rate parameters m_0 and m_1 was computed as follows:

$$L_x(m_0, m_1) = \sum_{i=1}^{n_x} \begin{cases} \ln(\lambda_{c_i, f}) t_i + (\lambda_{c_i, f}) t_i & \text{for } t_i < 9 \\ (-\lambda_{c_i, f}) t_i & \text{for } t_i = 9 \end{cases} \quad (1)$$

where $\lambda_{c_i, f}$ is the expected mortality probability based on function f (i.e. either a constant or a linear function of colony size, c_i), n_x is the sample size, n , of each coral group $x = \{1, 2, 3, \text{ or } 4\}$, and t_i is the number of 6 mo time intervals until mortality occurred for individual i . Eq. (1) accounts for the fact that a colony could die during the study or survive throughout the duration of the study. Maximum likelihood estimates were generated for each mortality model and the significance of the size-dependent term of the log-linear model was determined based on a likelihood ratio test (Hilborn & Mangel 1997).

3. RESULTS

3.1. Patterns of coral dynamics

Percent coral cover (expressed as the fraction of the benthos covered by corals divided by the total cover of the benthos) remained stable throughout the study period at a level of $4.0 \pm 0.7\%$ (\pm SD; 1-way ANOVA: $F_{8,602} = 0.7$, $p = 0.69$). Average (\pm SD) percent cover and colony density during the study period for each of the 4 coral groups was $1.2 \pm 0.27\%$ and 9.9 ± 2.2 colonies m^{-2} for *Madracis mirabilis*, $1.5 \pm 0.13\%$ and 3.3 ± 0.2 colonies m^{-2} for mounding corals, $0.5 \pm 0.09\%$ and 2.1 ± 0.4 colonies m^{-2} for *Agaricia agaricites*, and $0.8 \pm 0.2\%$ and 4.3 ± 0.4 colonies m^{-2} for *Millepora* spp. However, despite the apparent relative stability in overall coral cover through time, a comparison of average cover change in individual

colonies due to the various demographic fates revealed highly active demographic dynamics (i.e. corals experienced significant growth, shrinkage, fission, fusion etc.) throughout the same time period (1-way ANOVA: $F_{7,2355} = 13.35$, $p < 0.001$; Fig. 2).

Percent cover changes due to fission and fusion dynamics were particularly prevalent during the middle of the time series (~2010–2012), while percent cover changes related to colonies becoming covered by sediment or algae (negative change) to later re-emerge (positive change) occurred mostly from 2009 to 2010 and from 2012 to 2013 (Fig. 2). Notably, for most of the study, positive change in percent cover attributed to the demographic category of re-emergence of colonies was greater than negative change. This result likely stems from continued colony growth during the time that coral remained covered by sediment or ephemeral blooms of the macroalgae *Dictyota* spp.

3.2. Proportional colony growth as a function of initial colony size

Overall, proportional colony growth was generally positive for smaller colony sizes and approached zero towards larger sizes (Fig. 3). This result held for most demographic fate categories, specifically for the colonies experiencing isolated growth or shrinkage, fission, or multi-fates, but not for those that underwent fusion. For colonies that underwent fusion (blue dots in Fig. 3), average proportional colony growth was mostly positive in all coral groups for all sizes.

Our size-class-based approach revealed that the average relative growth of colonies $< 1 \text{ cm}^2$ was positive in all coral groups (Fig. 4a–d). The average relative growth of intermediate and larger size classes peaked near the zero-change line, indicating little to no relative growth (Fig. 4e–h), with the largest colonies exhibiting left-skewed proportional growth distributions (Fig. 4i–l). Fission, fusion, and multi-fate dynamics occurred across all colony size classes of *Madracis mirabilis*, and in intermediate and larger colony size classes of *A. agaricites* and *Millepora* spp., but rarely in the mounding coral group (Fig. 4, pie graphs). In *Madracis mirabilis*, 26.5% of all surveyed colonies experienced fission/fusion/multi-fate dynamics, while only 4.6% in mounding corals, 12.1% in *A. agaricites*, and 17.5% in *Millepora* spp. did. The proportion of colonies involved in fission, fusion, and multi-fate events increased with increasing colony size for *Madracis mirabilis*, from 9% in small colonies to 45% in the larger colonies, while for

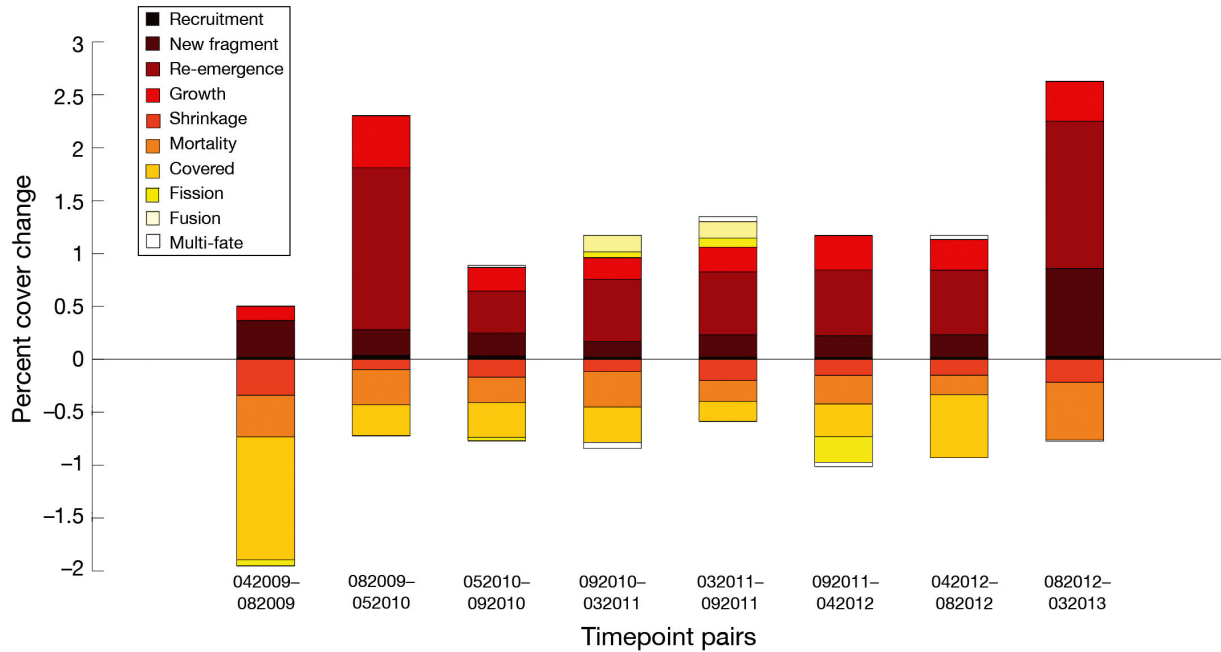


Fig. 2. Total coral percent cover change stemming from various coral colony demographic processes underlying a relatively steady overall percent coral cover time series. Timepoint pairs are labeled as the month and year (e.g. 042009 is April 2009) of the 2 consecutive surveys over which percent cover change is calculated

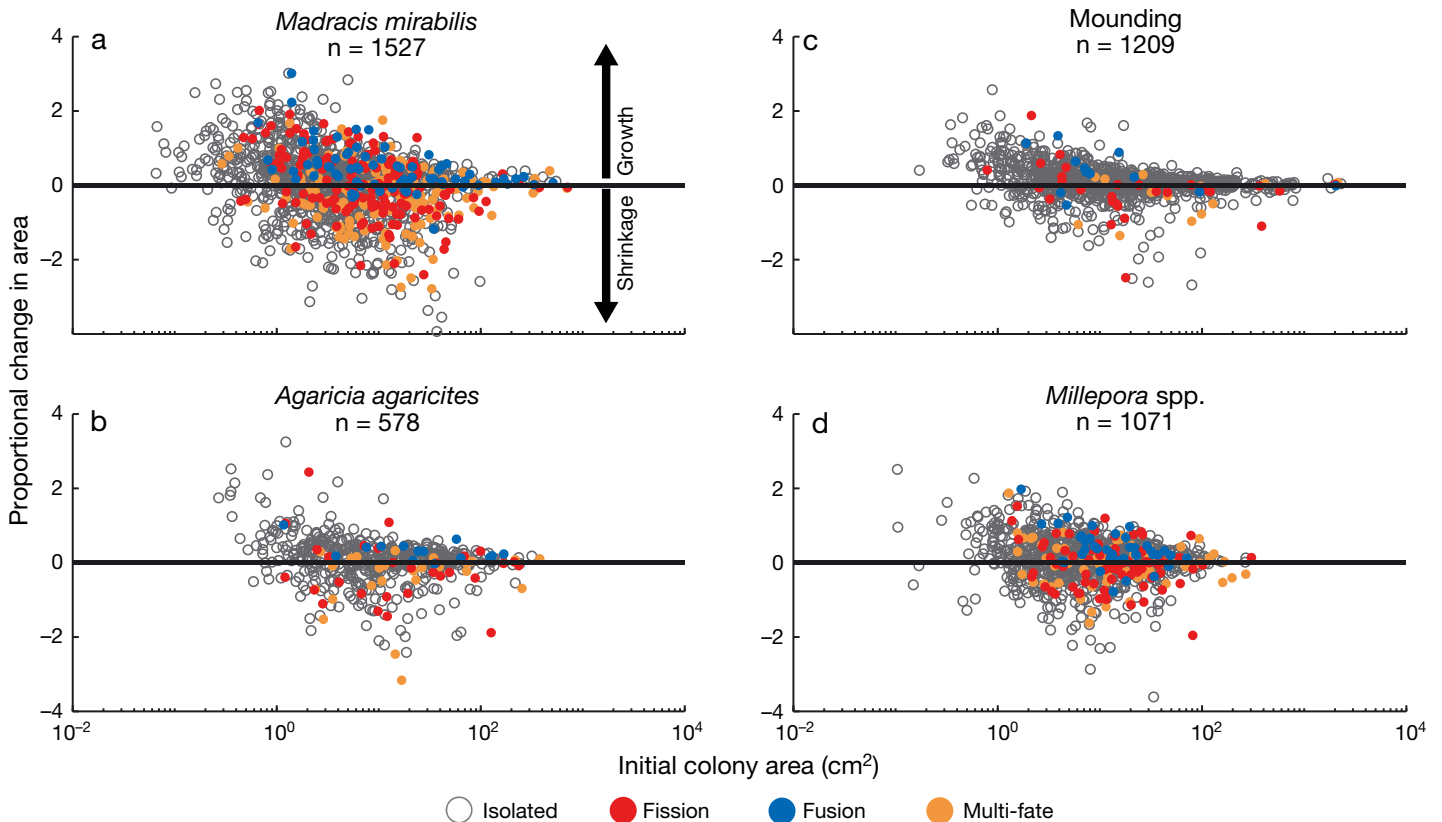


Fig. 3. Proportional change in coral colony area vs. initial area for all timepoint pairs of the 4 coral types: (a) *Madracis mirabilis*, (b) *Agaricia agaricites*, (c) mounding corals, and (d) *Millepora* spp., by fate (isolated, fission, fusion, and multi-fate). Overall, the degree of areal change appears to decrease with increasing initial colony area, but fusion-influenced changes show a net positive effect. Horizontal black line is the zero-change marker, and n is sample size

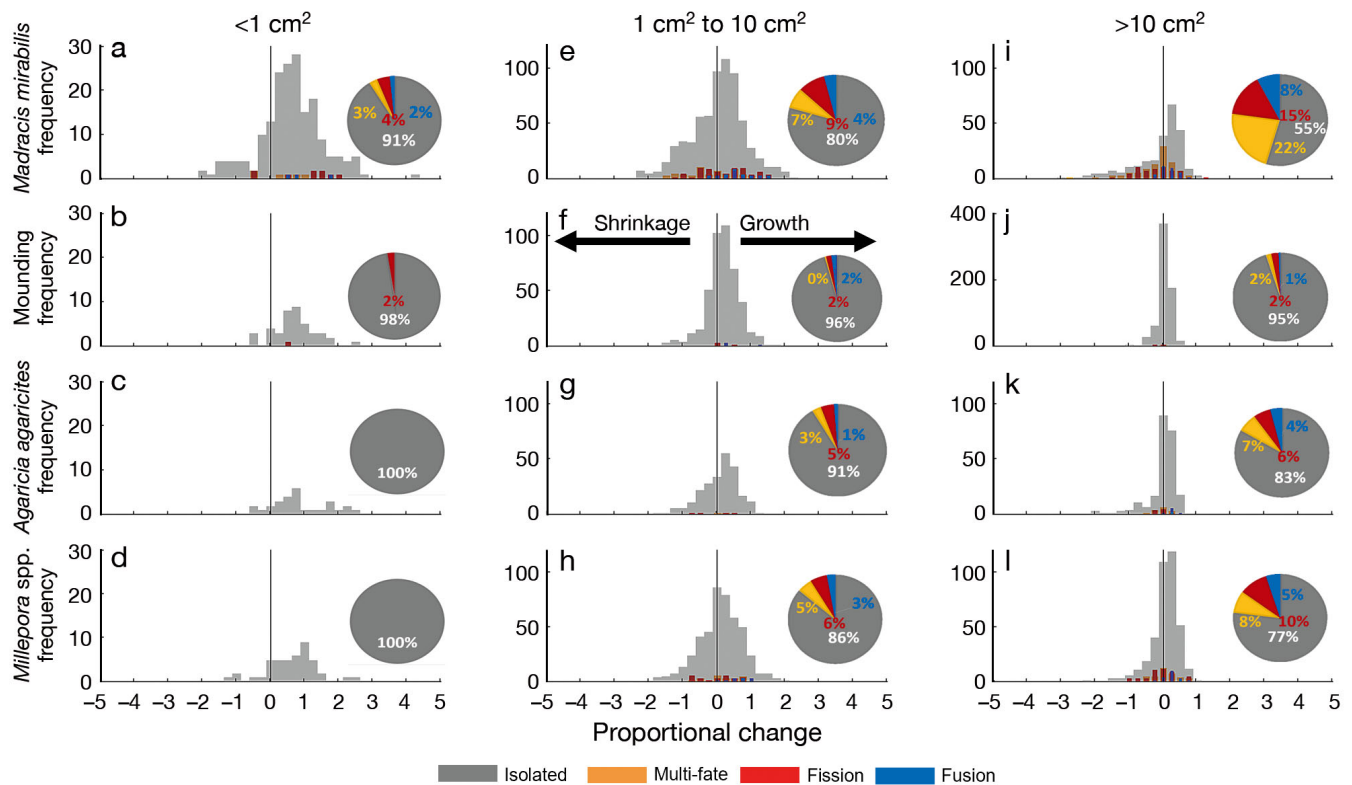


Fig. 4. Size-based distributions of proportional colony area change (difference of \log_e of colony areas) for all timepoint pairs across 4 yr. Shown are 3 \log_{10} size classes: (a–d) $<1 \text{ cm}^2$, (e–h) $1\text{--}10 \text{ cm}^2$, and (i–l) $>10 \text{ cm}^2$, for each of the 4 hard-coral types: (a,e,i) *Madracis mirabilis*, (b,f,j) mounding corals, (c,g,k) *Agaricia agaricites*, and (d,h,l) *Millepora* spp., by fate (isolated, multi-fate, fission, and fusion). Small size classes are dominated by positive growth, while intermediate sizes have both positive and negative change, and the largest size classes are left-skewed with more positive growth. Black vertical line marks zero change point. Pie charts show proportion of data exhibiting a particular fate; increasing size classes of *Madracis mirabilis* show the most notable increase in fission/fusion/multi-fate dynamics

all other groups, the difference across size classes was 2 to 5% for mounding, 0 to 17% for *A. agaricites*, and 0 to 23% for *Millepora* spp. Fusion events positively contributed to increases in colony growth in intermediate and large size classes, whereas fission and multi-fate processes generally contributed negatively to coral growth (Table 1).

3.3. Size-specific and fate-based longevity patterns

Longevity increased significantly ($p < 0.001$) with increasing colony size for all hard-coral groups that did not experience fusion, fission, or a combination thereof (Fig. 5a–d). For each coral group in the ‘iso’ fate category, size-dependent mortality was best described as a log-linear function of colony size, c : *Madracis mirabilis*: $\lambda_c = 0.54 - 0.08 \ln(c)$, mounding corals: $\lambda_c = 0.13 - 0.02 \ln(c)$, *A. agaricites*: $\lambda_c = 0.33 - 0.05 \ln(c)$, and *Millepora* spp.: $\lambda_c = 0.34 - 0.06 \ln(c)$. An example of the degree to which larger colonies

experienced decreased mortality probabilities is captured for mounding types in which 95% of colonies $>64 \text{ cm}^2$ survived 1.5 yr or more (Fig. 5b). A non-significant relationship between mortality probability and colony size was found for colonies experiencing fission, fusion, or multi-fate dynamics, except in *Madracis mirabilis*, which exhibited a weak negative relationship between coral size and the probability of mortality ($\lambda_c = 0.11 - 0.01 \ln(c)$) (Fig. 5e–h).

Overall, longevity was higher in colonies actively undergoing fission, fusion, and multi-fate dynamics, with 84% of colonies surviving 3.5 yr or more (Fig. 5e–h, bars are 84% red or dark red). In contrast, only 34.6% of isolated-fate colonies survived for 3.5 yr or more (Fig. 5a–d).

4. DISCUSSION

The negative relationship observed between proportional colony growth (i.e. relative change in area)

Table 1. Randomization results for effect of fate on colony proportional areal change, for 3 size classes (<1, 1–10, and >10 cm²) of each of the four 4 coral groups. Summary statistics for the effect of fate on proportional change corresponding to histograms in Fig. 4. Significant results (p ≤ 0.05) are in **bold** using fate-based color key in Fig. 4. Change resulting from fusion has a significant positive effect in medium and large colonies. Change from fission and multi-fate processes are negative. p: p-value from randomization (α = 0.05); Diff: difference between mean of isolated-fate-influenced change in area and mean of either multi-fate-, fission-, or fusion-influenced change in area, respectively; n: sample size; SD: standard deviation; na: not applicable; nd: no data

Coral group	Statistic	<1 cm ²			1–10 cm ²			>10 cm ²				
		Isolated	Multi-fate	Fusion	Isolated	Multi-fate	Fusion	Isolated	Multi-fate	Fusion		
<i>Madracis mirabilis</i>	p	na	0.349	0.211	0.537	na	0.166	0.101	na	0.400	0.452	0.003
	Diff	na	-0.361	0.393	0.320	na	-0.154	0.165	na	-0.077	-0.080	0.382
	n	185	6	9	3	683	63	79	254	105	70	36
	Mean	0.608	0.246	1.001	0.927	0.020	-0.134	0.185	-0.212	-0.289	-0.292	0.170
Mounding corals	SD	0.946	0.663	0.882	0.664	0.855	0.839	0.839	0.876	0.754	0.701	0.367
	p	na	nd	0.533	nd	na	0.102	0.186	na	0.028	<0.001	0.059
	Diff	na	nd	-0.308	nd	na	-0.596	0.217	na	-0.270	-0.452	0.227
	n	41	0	1	0	438	2	9	674	13	18	4
<i>Agaricia agaricites</i>	Mean	0.717	nd	0.409	nd	0.179	-0.417	0.396	0.003	-0.267	-0.449	0.230
	SD	0.639	nd	0.000	nd	0.483	0.903	0.671	0.330	0.493	0.625	0.468
	p	na	nd	nd	nd	na	0.023	0.561	na	0.023	0.106	0.030
	Diff	na	nd	nd	nd	na	-0.526	-0.111	na	-0.342	-0.248	0.307
<i>Millepora</i> spp.	n	28	0	0	0	244	8	12	236	19	17	11
	Mean	0.877	nd	nd	nd	0.108	-0.418	-0.003	-0.047	-0.389	-0.295	0.261
	SD	0.834	nd	nd	nd	0.623	0.645	1.051	0.517	0.896	0.682	0.192
	p	na	nd	nd	nd	na	0.466	0.613	na	0.577	0.059	0.116
<i>Millepora</i> spp.	Diff	na	nd	nd	nd	na	-0.097	0.066	na	-0.041	-0.141	0.145
	n	44	0	0	0	462	28	31	378	40	49	24
	Mean	0.629	nd	nd	nd	0.100	0.004	0.166	0.038	-0.002	-0.103	0.183
	SD	0.764	nd	nd	nd	0.668	0.722	0.971	0.469	0.424	0.562	0.386

and initial size confirms our expectation of geometrically constrained colony growth for all 4 coral groups. While corals in theory, and sometimes in the field, exhibit seemingly unrestricted growth, there are geometric and structural constraints. The observed reduction in relative colony growth with increasing size is due partly to geometry, as coral colonies growing in size experience a decrease in the amount of relative area grown per unit perimeter (Chadwick-Furman et al. 2000, Pratchett et al. 2015, Dornelas et al. 2017). We do acknowledge that this pattern does not necessarily apply to predominantly vertically extending large branching coral species, like *Acropora* spp. which have been observed to have linearly increasing growth rates (Guzner et al. 2007). Nonetheless, the results discussed below reveal how life history strategy, morphology, and demographic processes ('fates') predictably influence relative colony growth rates, complementing effects linked to geometric expectations based on size alone.

Madracis mirabilis, the most abundant coral at this site, illustrates how a weedy life history strategist, with a branching morphology prone to fragmentation, can maximize positive areal change by fragmenting into smaller colonies capable of faster proportional growth. By actively undergoing fission and fusion, these smaller colonies have a lower mortality probability relative to that typical of larger corals. The absence of size-dependent survival in fragments of *M. mirabilis* corals has been observed before in Jamaica, where fragment survivorship depended foremost on environmental context, with higher survivorship in forereef sites compared to lagoons (Bruno 1998). In the present study, *M. mirabilis* was the taxon with the highest incidence of fission/fusion/multi-fate dynamics (26.5% of all surveyed colonies) and the group with the highest increase in the proportion of colonies actively undergoing fission and fusion with increasing colony size. This makes sense, as we might ex-

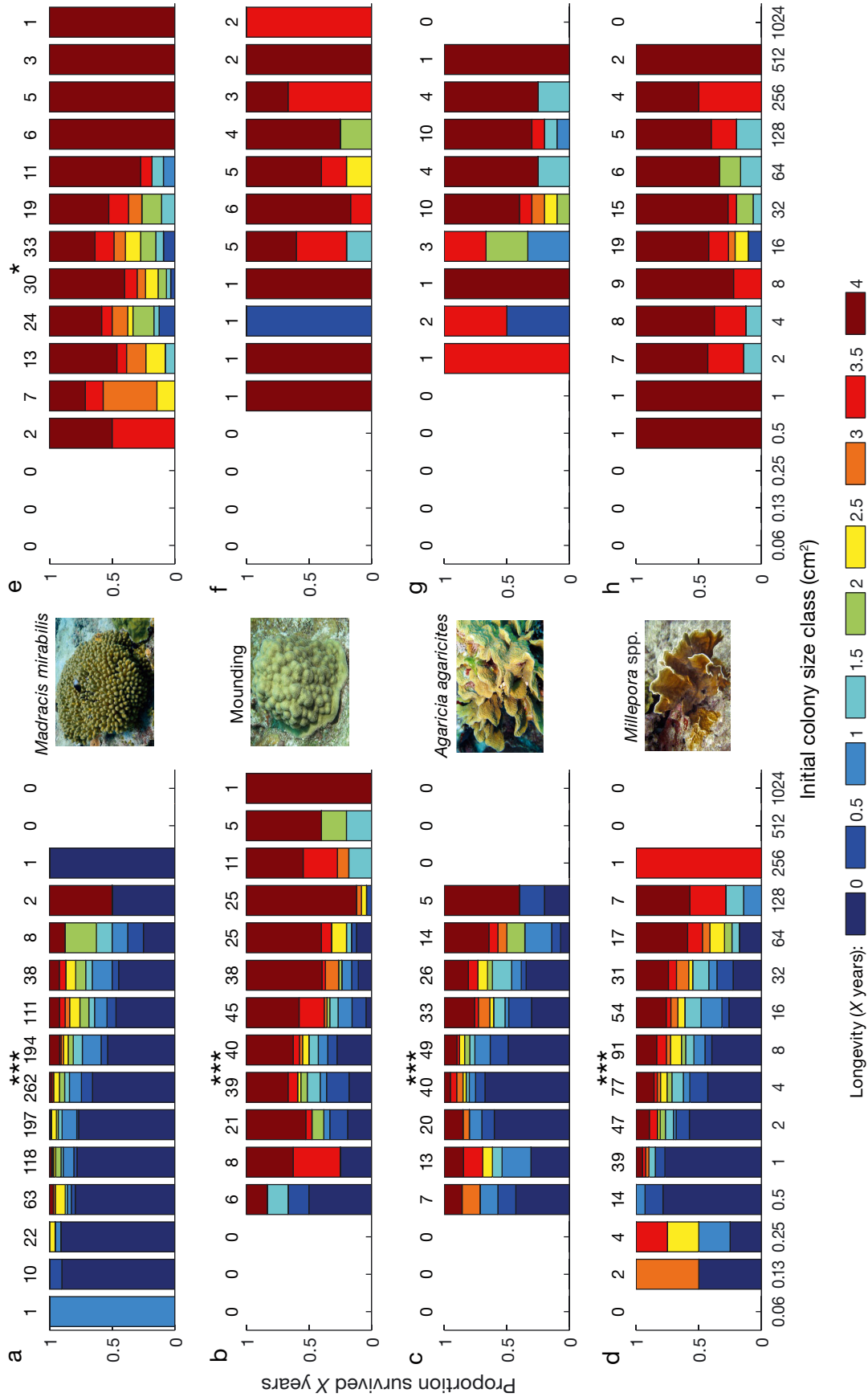


Fig. 5. Proportion of colonies surviving for each longevity category (refer to color key) as a function of initial size. For each hard-coral group: (a,e) *Madracis mirabilis*, (b,f) mounding corals, (c,g) *Agaricia agaricites*, and (d,h) *Millepora* spp., data was divided into 2 general fate categories: (a–d) isolated and (e–h) fission/fusion/multi-fate. Significant size-dependent longevity occurs in isolated change colonies, which disappears in colonies with fission/fusion/multi-fate dynamics, that exhibit significantly increased longevity overall. Significant maximum likelihood-based log-linear relationships between longevity and size: * $p < 0.05$; *** $p < 0.001$. Values above bars are sample sizes. Note: x-axis is log₂ scale

pect larger colonies to have more branches susceptible to fragmentation. Active fission and fusion processes in this weedy, branching species increased growth and longevity, which contributed to the species' local persistence. *M. mirabilis* was the only coral type for which colonies retained a (albeit weak) size-dependent mortality under active fission and fusion dynamics, whereas such size-dependent mortality was not observed in all other coral types. Reduced size-dependent mortality among fragmenting and fusing colonies contributes to an increase in the amount of related small colonies on a reef that could lead to a size bias favoring survival of smaller colonies relative to larger colonies.

Mounding corals often exhibit a stress-tolerant (*K*-selected) life history strategy typical of hardy, long-lived corals (Murdoch 2007, van Woesik et al. 2012). The majority of mounding colonies in our study occurred in the intermediate and larger size classes, whereas young corals and recruits were relatively rare compared to the other 3 coral groups considered. Mounding types also had the greatest proportion of colonies alive throughout the entire study period but had lower relative growth overall without undergoing much fission or fusion (4.6% of all surveyed colonies). Numerous studies and references therein have also reported slower growth in mounding colonies compared to other coral types (e.g. Dullo 2005, Darling et al. 2012), with e.g. Soto-Santiago et al. (2017) showing a tendency for *Orbicella annularis* and *Porites astreoides* to remain in the same size class for longer periods of time rather than transitioning to larger size classes. Comparable rates of fission and fusion in mounding corals include <5% in the Gulf of Oman (Foster & Foster 2013) and 1% and 6% in 2 sites in Australia (Babcock 1991). In fact, fission and multi-fate dynamics negatively affected growth in mounding colonies in the present study. This result could be linked to the extent of tissue loss after fission, whereas large distances between the resulting sub-colonies combined with slower colony growth rates overall would preclude fusion at a later time.

As with other corals examined to date, colony growth depended on colony size in *Agaricia agaricites* and *Millepora* spp., indicating that size-dependent growth occurs in both scleractinian and hydrozoan corals (Chadwick-Furman et al. 2000, Pratchett et al. 2015, Dubé 2016, Dornelas et al. 2017). Both taxa exhibited strong negative size-dependent mortality, a relationship that, like in *Madracis mirabilis* and mounding types, disappeared for colonies undergoing fission, fusion, and multi-fate dynamics. This strongly indicates that fragmented colonies retain their higher

survival probabilities after being a part of larger colonies or from potential positive effects on colony performance after fission and/or fusion. Additionally, notable similarities between *A. agaricites* and *Millepora* spp. were reflected in nearly identical parameter values defining their log-linear size-dependent mortality functions. Similar morphology-based size-dependent mortality relationships have been previously linked to colony modularity, where larger modular organisms are more likely to experience partial mortality rather than whole-colony mortality, unlike small colonies (Connell 1973, Jackson 1979, Hughes & Jackson 1985, Hughes & Connell 1987). In addition to monotonically decreasing mortality relationships with colony size, recent studies of larger branching species susceptible to biomechanical dislodgement have been described with quadratic (or 'bathtub') shaped functions (Madin et al. 2014). The similarities in growth and mortality dynamics of colonies sharing a foliose morphology, but belonging to corals and hydrocorals, further supports a morphologically based approach to coral community demography (Murdoch 2007, Dornelas et al. 2017).

We found a strong presence of fusion/fission dynamics on coral colony growth experienced by 16.4% of the total number of colonies that were monitored, a value that appears comparable to values reported for other species and locations. Hughes & Jackson (1985) found the mean annual probability of fission in Jamaican foliaceous corals to vary between 2 and 10% and for fusion between 1 and 6%. Elahi & Edmunds (2007) found a fission rate of 42% of *Siderastrea siderea* colonies. Part of the reason for considering fission and fusion together is that they often occur as multiple sequential events in the life of a single coral colony (hence, our multi-fate category), especially in branching coral species like *Madracis mirabilis*. Overall, the positive and negative proportional growth experienced by colonies as a result of fission or multi-fate dynamics suggests that breaking into smaller fragments increases coral perimeter exposure to competitive interactions that result in growth or shrinkage. The mostly positive growth effect experienced by small colonies that underwent fusion suggests that combining into larger contiguous coral units might have benefits (e.g. resource sharing, increased survival) that outweigh the geometrically constrained growth of larger colony sizes (Raymundo & Maypa 2004). That survival significantly increased for colonies actively undergoing fission, fusion, and multi-fate dynamics regardless of coral type captures the demographic advantages of a clonal life history strategy in the face of external disturbances.

Combining quantitative size-dependent demographic patterns of coral colonies based on size structure and morphology contributes to a better understanding of changes in coral community structure, even when the net change in total coral cover across a reef appears to be zero. We have included both geometric and biologically based mechanisms to explain colony size-dependent growth and survival and show the influence of fission and fusion on those rates. Elucidating colony-level dynamics and processes underlying percent coral cover change also allows a more mechanistic approach to gauging the direction of future changes in coral community composition and structure. Overall, our results confirm earlier studies demonstrating size-dependent demographic growth and survival rates for scleractinian coral colonies (Hughes 1984, Zilberberg & Edmunds 2001, Ferrari et al. 2012, Kayal et al. 2015, Álvarez-Noriega et al. 2016, Dornelas et al. 2017). Similarly, our findings have implications for other modular benthic marine invertebrates, such as ascidians, sponges, zoanthids, bryozoans, and gorgonians, that exhibit similar dynamical growth patterns to corals (i.e. they grow, shrink, and undergo fission and fusion). Lastly, these findings illustrate the usefulness of size-dependent, life-history and morphologically focused demographic approaches to understand community dynamics within benthic systems of colonial organisms that go beyond traditional approaches that quantify solely the net outcome of such dynamics.

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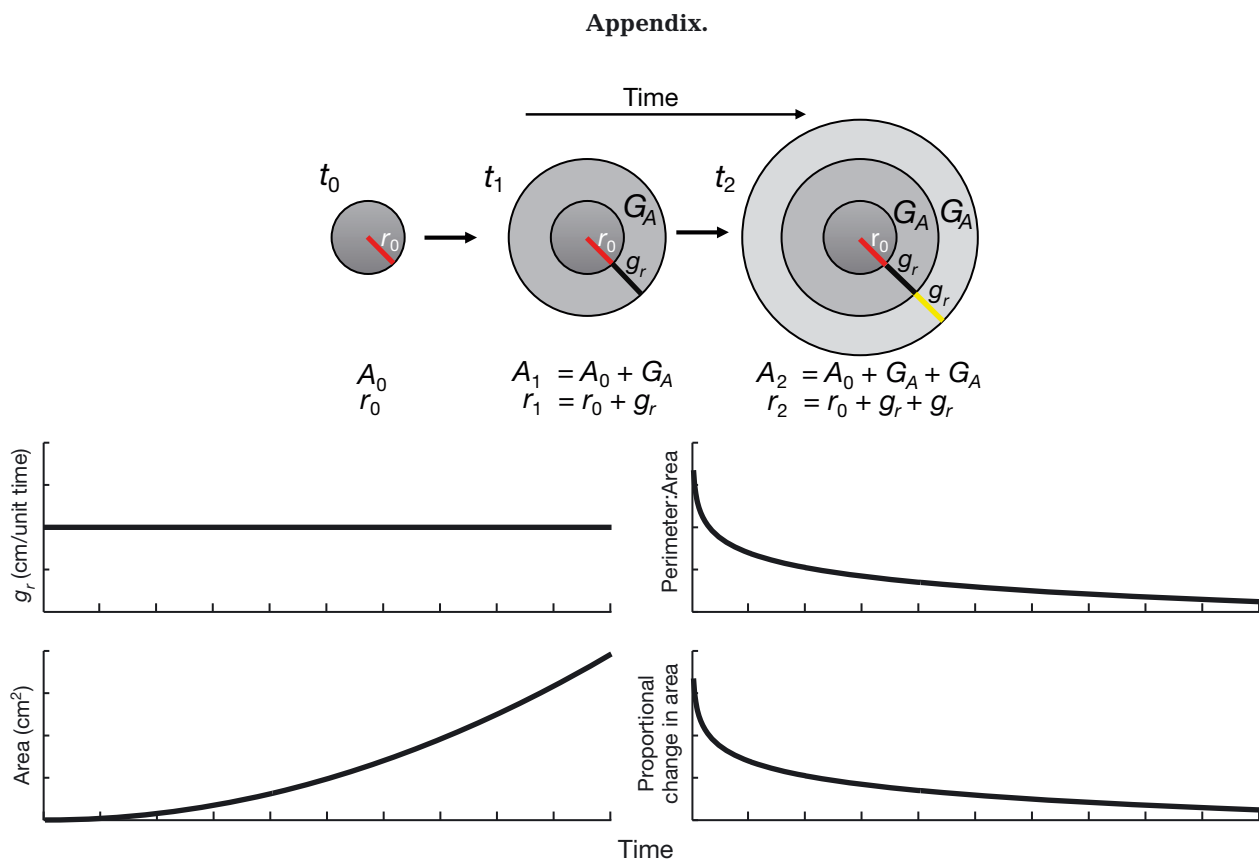


Fig. A1. Theoretical growth expectations based on geometric constraints. Theoretical geometric-based constraints in growth for circular colonies with constant radial extension. As colony size (total area, A) increases, the perimeter-to-area ratio and the proportional change in area decrease. t : time-point; r : radius; g_r : growth rate; G_A : area resulting from growth interval