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coral reef paper

Environmental and biological determinants of the size, shape, and orientation of coral bommies in the back reef of Moorea, French Polynesia

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ABSTRACT.—On shallow coral reefs, coral bommies create patchy communities where interactions among patches are likely to affect a variety of ecological features. Here, we describe bommies in the back reef of Moorea, French Polynesia, and evaluate the role of select factors in determining their size, shape, and distribution. We tested the hypothesis that the distribution and growth of corals varies across the surface of bommies (i.e., north, south, east, and west sides), and therefore might play a role in determining bommie shape and their propensity for fission and fusion. Bommies were elliptical in planar shape, with their long axes parallel to ambient flow and perpendicular to the direction of offshore waves. *Porites* spp. and *Pocillopora* spp. were the most abundant corals, and they were uniformly distributed over the surface of bommies. During April 2022, small colonies (≤4 cm height) of *Pocillopora* spp. grew at similar rates on the north, south, east, and west sides of the bommies, among which integrated seawater flow during the experiment was similar. These results suggest that the contemporary growth and distribution of corals is unlikely to play a strong role in determining the features of present-day bommies. Evaluating how environmental conditions mediate the structure of coral bommies in shallow habitats will help to understand whether habitat mosaics can mediate coral reef resilience in the Anthropocene.

Climate induced variation to the extent to which ecosystems exhibit patchiness has motivated scrutiny of how these systems will respond to further environmental change (Rietkerk et al. 2021). One outcome of this scrutiny is the discovery that patchy ecosystems can provide early warning of ecological degradation (Rietkerk et al. 2004), for example, through an increased number of small habitat patches (Scheffer et al. 2009). Small (<1 km^2) and structurally complex habitat patches have elevated conservation value compared to larger patches, which can exhibit lower complexity (Wintle et al. 2019). Contrasts of the ecological value of multiple small, versus a few large, habitat patches have shown that ecological diversity can be maintained by small patches in disturbed environments, with the structural characteristics playing a critical role in this association (Fahrig 2003, 2013). Studies of these effects have focused on terrestrial ecosystems (Haddad et al. 2015, Arroyo-Rodríguez et al. 2017) to highlight the general concept that small patches of habitat can provide suitable locations for organisms in otherwise uninhabitable areas (Levin and Paine 1974, Pickett and Thompson 1978). In such cases, the shape, distribution, and size of habitat patches at small spatial scales can determine the probability of functional collapse of the ecosystem (Rietkerk et al. 2021).

On tropical coral reefs, habitat patchiness has been evaluated with respect to effects on kilometer-scale benthic community structure (e.g., Huntington and Lirman 2012, Adjeroud et al. 2019) and the diversity of reef fishes with which it is positively associated (Nanami and Nishihira 2003). In Moorea, French Polynesia, the shallow back reef provides a patchy environment (sensu Anderson et al. 1981) with numerous coral bommies of varying size and dimensions (i.e., community patches) that are interspersed with areas of sand and reef rock. The term "coral bommie" is entrenched in reef literature (Anderson et al. 1981, Schmitt et al. 2022), and here we use "bommie" to describe emergent carbonate structures in the back reef that are built mostly of living and dead colonies of massive *Porites* spp. This carbonate reef structure is susceptible to biotic and abiotic processes which can alter the structure and distribution of the reef habitat. Water flow impacts the growth of coral colonies (Chindapol et al. 2013) and whole bommies (Hein and Risk 1975), and seawater chemistry can affect the dissolution of their calcium carbonate framework (Silbiger et al. 2014). Biotic factors like the growth of calcifying organisms (Wei et al. 2022), and the partial mortality and fission of coral colonies (DeVantier and Endean 1989, Roff 2020), can further influence the shape and structure of bommies (Wei et al. 2022). In back reef habitats, the shape and size of coral bommies can affect the diversity of corals and other organisms with which they are associated on a meter scale (Idjadi and Karlson 2007, Hamman 2019).

In this study, our objective was to explore the role of present-day coral communities in contributing to the structure of coral bommies in the lagoon of Moorea. To quantify the ecological and physical environment, we first described the shape and orientation of bommies to evaluate whether their planar shape was asymmetric relative to the reef crest. We then tested the hypothesis (H1) that corals are distributed nonrandomly over bommies with respect to their orientation relative to ambient seawater flow. We sought insight into drivers of bommie structure by conducting two short experiments to test the hypotheses that the growth rate of corals (H2) and integrated seawater flow (H3) differ around the perimeter of bommies.

Methods

This study took place at three sites in the north shore lagoon of Moorea, French Polynesia (17°32′25.43″S, 149°49′55″W), during April and May of 2022 (Fig. 1). Given historical data showing that this lagoon is characterized by heterogeneous environmental conditions (Leichter et al. 2012, Dișa et al. 2022), sites were selected to sample this variation at 3 m depth and 100–150 m from the reef crest. Sites were standardized for distance from the reef crest because seawater flow is predominantly unidirectional across this reef and is driven by offshore wave forcing (Hench et al.

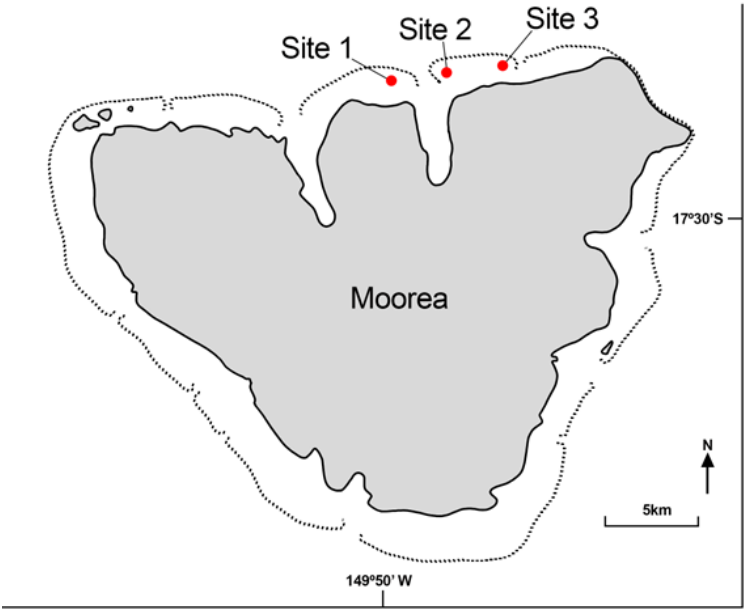

Figure 1. Map showing approximate location of the three study sites (red dots) on the north shore of Moorea.

2008). The fixed distance of bommies from the reef crest increased the likelihood that they were exposed to similar flow regimes (Hench et al. 2008), which can be an important physical force determining bommie structure (Mass and Genin 2008, Chindapol et al. 2013, Hench and Rosman 2013). The prominence of unidirectional flow motivated sampling of bommies by planar quadrants oriented around their long axes that were approximately perpendicular to the reef crest (Fig. 2A). The coral communities on the bommies were sampled in each of four quadrants that had unique positions relative to the direction of the prevailing flow (Fig. 2A). To select bommies for analysis, 30 m transects were haphazardly laid parallel to the reef crest at each site (5 transects site^{-1}), and all bommies intersecting each transect were surveyed. Individual bommies were treated as statistical replicates using quadrants on the bommies and site as fixed effects in the statistical model (described below).

Shape and Orientation of Bommies.—The planar length and width of each bommie, as well as the height from the benthos to the highest point on each bommie (n = 79), was recorded with a flexible tape (1 cm). Measurements were recorded adjacent to the sand and reef rock at the base of each bommie, thereby allowing the maximum size to be recorded. The angular orientation of their primary axis relative to the reef crest (Fig. 2B) was measured using a hand-held compass (±1°).

H1: Coral Distribution.—Bommies were surveyed for coral community structure by counting corals (>4 cm diameter) by genus within each quadrant (Fig. 2A) using a randomly placed quadrat (0.25 m^{-2}). Statistical analyses were conducted in the R software environment (v4.2.3; R Core Team 2020) using a randomized block PERMANOVA (adonis2 in the VEGAN package, Dixon 2003) to test for variation in

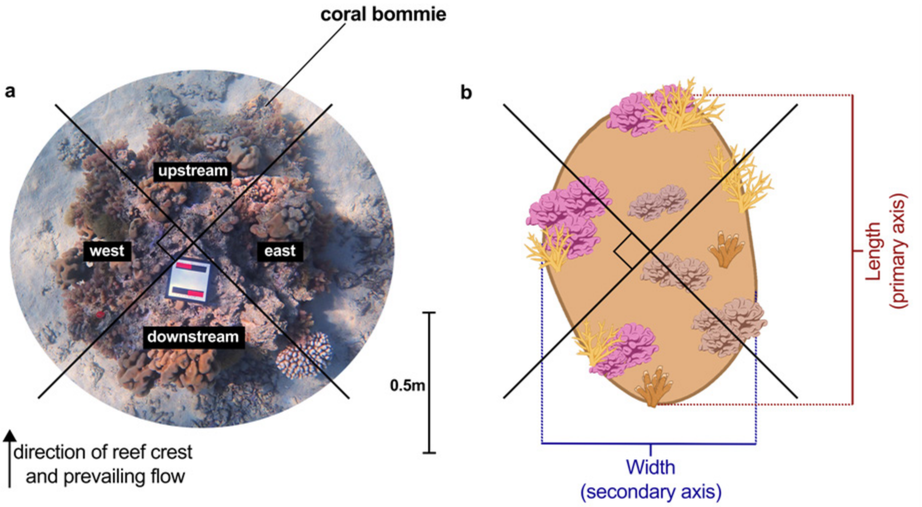

Figure 2. Schematic showing the distribution of bommies in Moorea and the approach applied in the present study to their analysis. (A) Representative bommie with an elliptical planar shape and a primary axis perpendicular to the reef crest and parallel to the prevailing flow from the north. (B) Example of how bommies were divided into quadrants relative to the ambient flow and within which corals were surveyed for density and growth and flow speed measured. Coral icons illustrate the distribution of colonies of *Porites* spp., *Pocillopora* spp. and *Acropora* spp. on the four sides of the bommie. Artwork by A Dahl.

the density of corals (colonies 0.25 m^{-2}) around the bommies. Bommie, quadrant, and site were fixed effects, and bommie was the blocking factor. A PERMANOVA was used because the data did not conform to parametric assumptions.

H2: Growth Rate of Corals.—To test the hypothesis that the growth rate of corals varied around the perimeter of bommies, nubbins (n = 52 single branches, about 4 cm in height after Davies 1989) of *Pocillopora* spp. (excluding *Pocillopora acuta*) were deployed on 13 bommies that were randomly selected, with four at sites 1 and 3, and five at Site 2 (Fig. 1). *Pocillopora* spp. was studied because its corymbose structure is representative of a common morphological group of branching corals (Veron 2000), it is easy to fragment (Birkeland 1976), and is abundant in Moorea (Tsounis and Edmunds 2016). One branch was randomly sampled from each *Pocillopora* spp. colony, and colonies were randomly selected with the constraint of being outside of the areas surveyed for bommie features.

Nubbins were prepared by fixing branches upright to plastic platforms using epoxy (Z-Spar, A-788 Splash Zone Compound), applied with minimal contact of live tissue. Buoyant weight was recorded before deployment (±1 mg resolution; PR 224 Series Balance, OHAUS, Parsippany, New Jersey, USA) and then the plastic platforms were secured to cement blocks placed around bommies adjacent to the survey areas. Four nubbins were randomly placed within each quadrant of each bommie, and their growth rate was assessed from change in buoyant weight (Jokiel 1978) over 20 days using each nubbin as a statistical replicate. Change in buoyant weight was converted to dry weight using an aragonite density of 2.93 g cm^{-3} (Davies 1989), and an empirical determination of seawater density (mean = 1.022 g cm^{-3}). Growth rates were normalized to time and surface area (mg cm^{-2} d^{-1}), with area determined by two-layer wax dipping (Stimson and Kinzie 1991). Growth (mg cm^{-2} d^{-1}) was analyzed using a randomized block ANOVA in which site and treatment (quadrant) were fixed effects, and bommie was the blocking factor. Data were assessed for normality and homoscedasticity using a graphical analysis of residuals and were log (x + 1) transformed where necessary (Quinn and Keough 2002). Statistical analyses were conducted using R statistical software (R base package, v4.2.3; R Core Team 2020)

H3: Integrated Flow Around Bommies.—To test the hypothesis that seawater flow varies around the perimeter of the bommies, integrated water motion was measured using 120 clod cards (Doty 1971, Thompson and Glenn 1994) placed around 30 bommies for 24 hrs. Clods were made from a 1:5 mix of water and Plaster of Paris (DAP®, DAP Products Inc., Baltimore, Maryland, USA), molded into ice cube trays (with each block 4.0 × 3.0 × 4.2 cm). The clods were dried to a constant weight (at 60 °C), before weighing (±1 mg) and deploying to the bommies. Clods were deployed on 10 bommies randomly selected at each site on 7 April, 2022, and placed within each of the four quadrants on each bommie (Fig. 2A). These bommies represented the size range found in the lagoon of Moorea, with the smallest 77 × 73 cm, and the largest 265 × 221 cm. Clods were immersed for 24 hrs with controls placed in buckets of seawater, and dissolution (g h^{-1}) was calculated after proportional correcting for control dissolution (Brown and Carpenter 2015). The rate of dissolution was calculated by subtracting oven-dried final mass from the initial corrected mass (g d^{-1}) and was analyzed using a randomized block ANOVA in which site and treatment (quadrant) were fixed effects, and bommie was the blocking factor. Data were assessed for normality and homoscedasticity using a graphical analysis of residuals and were log (x + 1) transformed where necessary (Quinn and Keough 2002). Statistical analyses were conducted using R statistical software (R base package, v4.2.3; R Core Team 2020).

Results

Shape and Orientation of Bommies.—Bommies were about 1–10 m apart, they varied from 32 to 302 cm in length, 27 to 260 cm in width (Fig. 3), and they extended above the adjacent reef, often nearly to the surface of the water (i.e., a height of 1–2 m). Most bommies were rugose, dissected by deep fissures, and populated by a variable number of corals. Some were almost entirely covered by live corals, while others were denuded and covered by turf and macroalgae. At three sites, 79 bommies were surveyed, and all were asymmetric in planar shape with a mean (SE) length of 1.24 (0.02) m. The elliptical bommies aligned relative to the reef crest to the north (0° at sites 1 and 3, 10° at Site 2; Fig. 1), and the prevailing direction of offshore waves, with the primary axis having a mean (SE) bearing of 330° (16°; n = 64).

H1: Coral Distribution.—Some coral bommies were dominated by living *Porites* spp. that formed much of their antecedent structure, while a few appeared to be constructed of smaller colonies of *Acropora* spp., and *Pocillopora* spp. Some bommies had 100% coral cover, usually composed of *Porites* spp., and coral diversity was low (i.e., the cover was nearly monospecific). Most bommies were populated by a variety of corals, and sometimes at densities as high as 7 colonies 0.25 m^{-2} (Fig. 4). Four genera were the most abundant on the bommies, with *Porites*, *Montipora*,

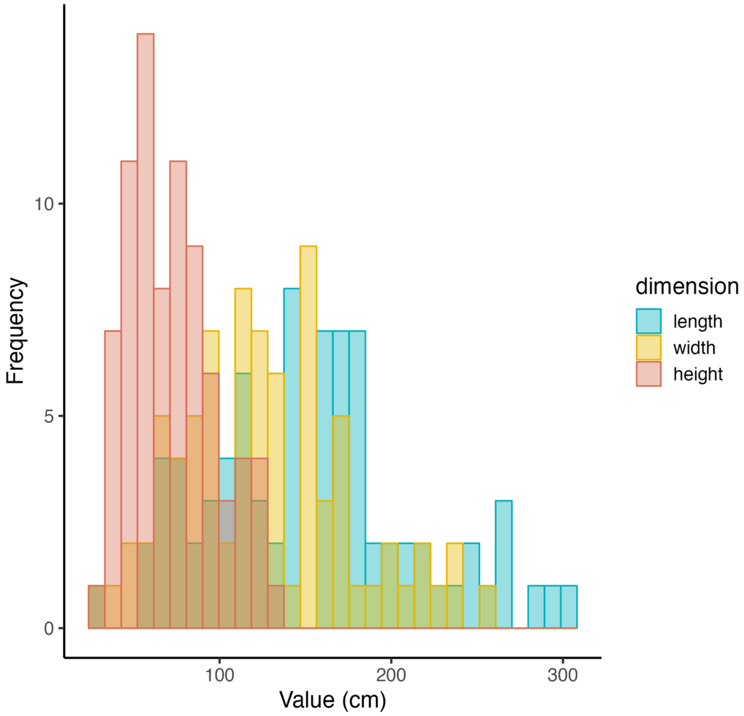

Figure 3. Histogram showing the frequency of bommie sizes based on their planar length, width, and height (cm; $n = 79$).

Pocillopora, and *Acropora* accounting for 90% of the corals ($n = 660$). Overall (pooled among bommies), 48% were *Porites* spp., 21% *Montipora* spp., 15% *Pocillopora* spp., and 6% *Acropora* spp. The remaining 10% belonged to other genera, of which *Pavona* spp. and *Psammocora* spp. were the most common. Mean (SE) densities of corals ranged from 0.21 (0.02) colonies 0.25 m^{-2} to 5.00 (1.79) colonies 0.25 m^{-2} ($n = 4$ quadrants per bommie, Fig. 4). The density of corals (pooled among taxa) did not vary among quadrants (i.e., upstream, downstream, west, east (Fig. 2B; PERMANOVA: pseudo-$F_{3,303} = 0.70$, $P = 0.22$) or sites (PERMANOVA: pseudo-$F_{2,303} = 16.22$, $P = 0.53$).

H2: Growth Rate of Corals.—Of the 52 nubbins placed on the bommies, 11.5% bleached or died during the 20-day study and were omitted from the analyses. Twenty-four nubbins (47%) showed signs of fish corallivory, and where these declined in weight by > 1 mg cm^{-2} d^{-1}, they were also excluded from the analyses (19 corals). With these exclusions, 27 *Pocillopora* spp. nubbins remained for the contrast of growth among quadrants (5–8 nubbins $quadrant^{-1}$, pooled among bommies), and these were scattered among 15 bommies. Their net growth varied from −0.71 mg cm^{-2} d^{-1} (i.e., they decreased in weight, in most cases with signs of fish bites to the corals or bases to which they were attached) to 9.57 mg cm^{-2} d^{-1}, and did not differ among quadrants ($F_{3,\ 9.6} = 0.79$, $P = 0.53$), or site ($F_{2,\ 6.4} < 0.01$, $P = 0.99$), with no significant interaction between quadrant and site ($F_{6,\ 9.6} = 1.26$, $P = 0.36$). Overall, mean (SE) coral growth was 3.87 (0.69) mg cm^{-2} d^{-1} (Fig. 5A).

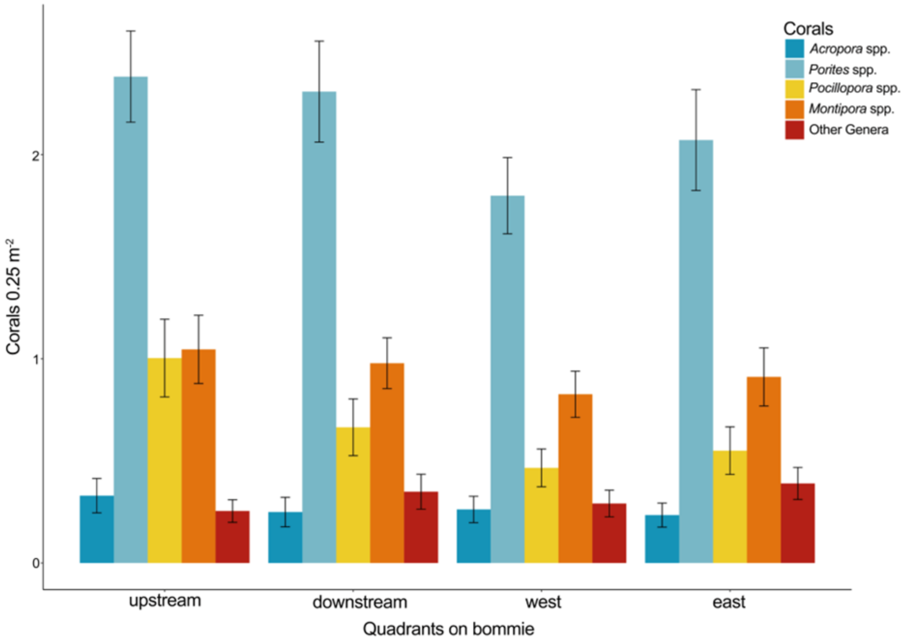

Figure 4. Bar graph showing mean abundances [colonies 0.25 m^{-2} (SE), $n = 76–79$] of corals in the four quadrants (Fig. 1) of bommies in the back reef of Moorea. Abundances shown for the four most common genera (*Acropora* spp., *Porites* spp., *Pocillopora* spp., and *Montipora* spp.) with the remainder pooled as "other".

H3: INTEGRATED FLOW AROUND BOMMIES.—Of the 120 clod cards deployed around 10 bommies site^{-1}, 4 were damaged in transit and 3 were attacked by fishes. These 7 were excluded from the analysis. During the 24 hrs deployment, clod dissolution did not differ among sides of bommies ($F_{3,101} = 1.68$, $P = 0.177$; Fig. 5B), but it varied among sites ($F_{2,101} = 22.19$, $P < 0.001$), and was greatest at Site 2 and lowest at Site 3. No significant effect of the interaction between side and site was detected ($F_{6, 101} = 1.32$, $P = 0.25$). Data files for this project are hosted on Dryad (https://doi.org/10.5061/dryad.jwstqjqk6).

DISCUSSION

Present-day reefs have been exposed to a wide spectrum of disturbances that are driving declines in coral cover (Alvarez-Filip et al. 2009, Eddy et al. 2018, 2021, Roff 2020) and the fragmentation of reef habitat (Knowlton 2001). Such fragmentation alters the structure of habitats and can lead to declines in biological diversity (Turner 1996). However, recent theoretical investigations have suggested that the effects of habitat fragmentation might not be as severe as anticipated (Rietkerk et al. 2021), especially if fragmentation is not associated with substantial habitat loss (Fahrig 2013). The evolving understanding of habitat patches and their associated communities (Rietkerk et al. 2021, Siteur et al. 2023) has emphasized that their current state, such as described here for coral bommies, might change under future climate conditions. We have begun to evaluate the structural asymmetry and ecological significance of habitat fragments in the shallow coral reef habitat of

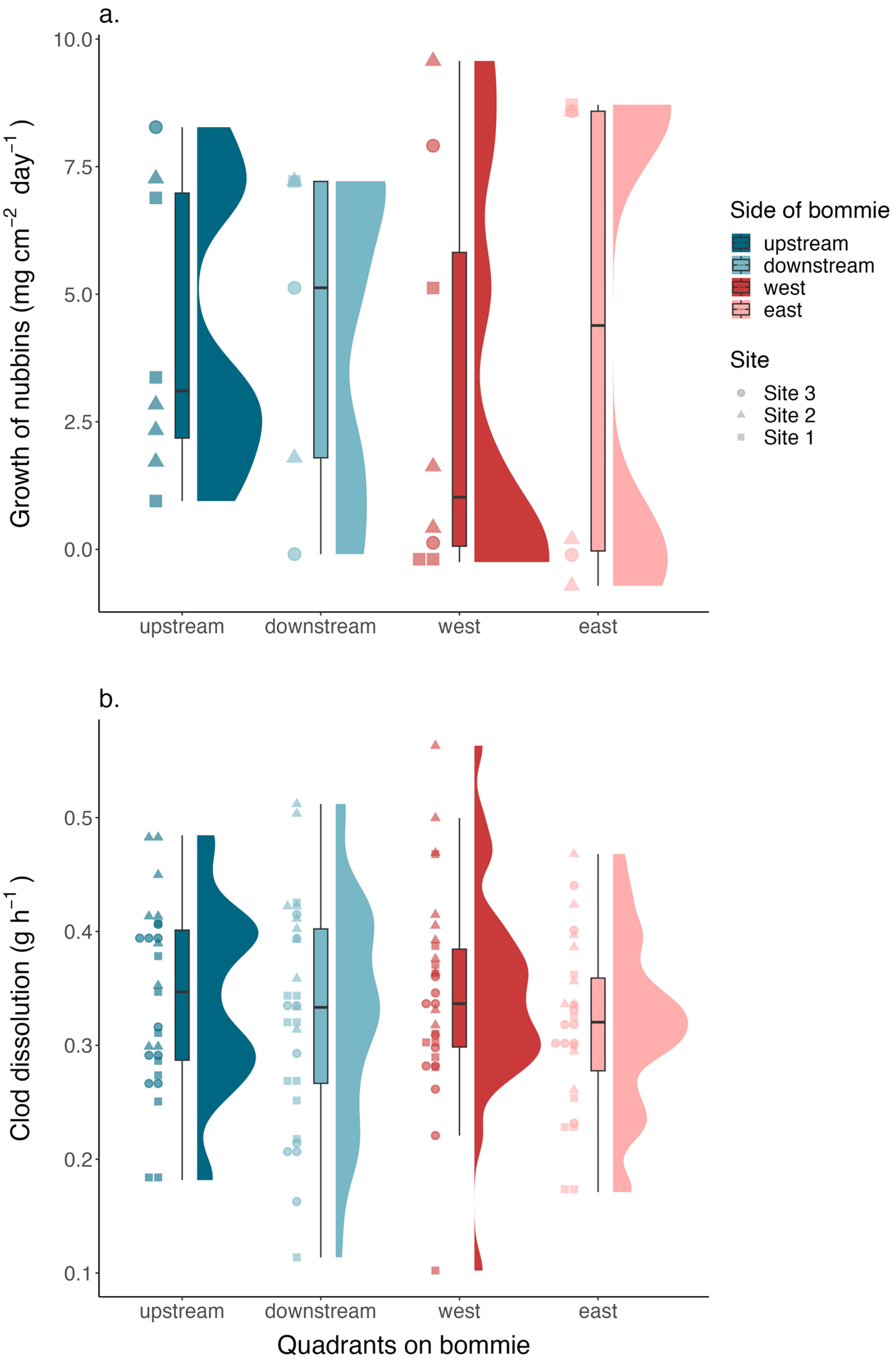

Figure 5. Variation in coral growth rate and integrated flow speeds among sides of bommies and across sites. Raincloud plot shows density of data, interquartile range, min, max, median (boxplot), and data points (scatterplot). (A) Growth of nubbins of *Pocillopora* spp. (mg cm^{-2} d^{-1}) over 20 days (n = 5–8 corals quadrant^{-1}) did not differ among quadrants or sites. (B) Integrated water flow [dissolution of clod cards (g h^{-1})] around four quadrants of bommies (n = 14–30 clods quadrant^{-1}) over a single day in April 2022. Dissolution did not differ among quadrants.

Moorea using bommies as examples of small habitat fragments in a patchy system. Our analyses reveal nonrandom shape asymmetry of bommies that vary in size, but tests of the likely causes of these effects returned null results for coral distribution, coral growth, and seawater flow. These findings do not provide definitive analyses of the mechanisms forming bommies, but they reveal the potential of bommies as a tractable system for exploring the theoretical implications of patchy habitats in the Anthropocene Epoch (Fahrig 2013, Rietkerk et al. 2021).

Our research suggests that bommie shape and size on present-day coral reefs may not be strongly determined by the contemporaneous distribution and growth of coral colonies on their surfaces (i.e., accretional processes). While early studies of coral bommies and patch reefs found that accretion and seawater flow influence patch formation (Stoddart 1969, Brown and Dunne 1980), these studies were completed in an era when the abundance of coral colonies and coral cover were higher than on most coral reefs in the 2020s (Cramer et al. 2021, Eddy et al. 2021). In contrast to the 1980s (and earlier), present-day bommies exist in an ecosystem typically depleted of the taxa from which they are built (i.e., scleractinians; Bruno and Selig 2007), and they are exposed to more frequent and intense disturbances (Edmunds 2019). It is possible that bommies in shallow lagoons are more likely to reflect the legacies of past accretion, dissolution, and erosion than the distribution and growth of extant corals. This possibility underscores the importance of studying structural legacies created by reef accretion and erosion to better understand the present-day structure and function of coral reefs (Kopecky et al. 2023).

Shape and Orientation of Bommies.—Asymmetry in the shape of patch reefs occurs on a scale of kilometers (Brown and Dunne 1980, Wei et al. 2022) and can be caused by several factors. At 10s–100s of meters, the asymmetric distribution of organisms can affect the shape of patches of reef that they create (Hamman 2019). The asymmetric growth of *Pocillopora verrucosa* colonies along their long planar axis produces elliptical colonies through flow-mediated growth in an environment with unidirectional seawater flow (Chindapol et al. 2013). Aggregates of asymmetrically shaped colonies are likely to have emergent properties when they are aligned, thus affecting the shape of the reef on which they grow. Changes to the morphology and distribution of corals can also result from their exploitation of available space on the benthos (Jackson and Buss 1975, Sandin and McNamara 2012). It is reasonable to expect that factors influencing the asymmetrical growth and distribution of coral colonies will also affect the overall structure of their habitat, resulting in patches of reef with asymmetric dimensions. As we describe below the present distribution and growth of coral colonies is unlikely to further accentuate asymmetric bommie shape.

H1: Coral Distribution.—Bommies and patch reefs are ubiquitous on shallow coral reefs in the Caribbean and Indo-Pacific (Jones 1977, Anderson et al. 1981) where they have a long history of investigation. Many of these studies have focused on the demersal fishes with which they are associated (Talbot et al. 1978, Sale 1980, Sale et al. 1994), or the benthic communities on their surfaces (Jones 1963, Sullivan and Chiappone 1992, Adjeroud 1997). While historic data highlights the non-random distribution of coral colonies as a mechanism contributing to the asymmetric shape of bommies (Garrett et al. 1971, Brown and Dunne 1980), in 2022 coral colonies occurred at equal densities on all sides of bommies in the lagoon of Moorea. While these present-day coral communities can perpetuate existing (i.e., antecedent) asymmetric bommie shape, the uniform distribution of coral colonies suggests they are unlikely to further alter bommie shape.

H2: GROWTH RATE OF CORALS.—The shapes and structure of coral bommies can also be affected by the rate at which coral colonies grow (Stoddart 1969, Dullo 2005). Rapid coral growth on one side of a bommie is likely to favor bommie asymmetry (e.g., making rhomboids), thus impacting the ways in which they interact with seawater flow (Hench and Rosman 2013). We measured the growth rates of *Pocillopora* spp. corals around several bommies and found no variation among sides, which is inconsistent with the notion that asymmetric growth of coral colonies favors the formation of bommies with irregular shapes.

Pocillopora spp. were selected for the measurement of coral growth because in 2022 they were abundant throughout the back reef of Moorea (Srednick et al. 2023). They are not, however, the foundation species (i.e., ecosystem engineers, sensu Dayton 1972) building bommies in this habitat, most of which are based on a framework of massive *Porites* spp. (Holbrook et al. 2002, Brown and Carpenter 2015). In 2022, live cover of massive *Porites* spp. was in decline in the back reef of Moorea (Srednick et al. 2023), thus favoring the choice of *Pocillopora* spp. for manipulative experiments. As the present measurements of coral growth were of limited scope, these results should be interpreted with caution.

H3: INTEGRATED FLOW AROUND BOMMIES.—Seawater flow over coral reefs is a strong physical force interacting with the physical structure of reefs (Hench et al. 2008, Reidenbach et al. 2021) affecting, for example, the mass transfer of metabolites between corals and seawater (Monismith 2007), and the frequency of fish corallivory (Lenihan et al. 2011, 2015). Moreover, the flow of seawater has the potential to create feedback between the growth of coral colonies and the growth of bommies (Reidenbach et al. 2009, 2021, Chindapol et al. 2013), in which changes in bommie shape modulate the ways in which coral colonies on their surface are affected by flow. The scale of these effects is illustrated by comprehensive measurements of seawater flow around bommies in the lagoon of Moorea (Hench and Rosman 2013), which show that flow speeds are 400% greater 2.4 m from bommies versus 0.4 m from bommies, at least during the austral summer. The measurements of integrated flow in the present study probably did not have the resolution to detect such effects (i.e., as in Hench and Rosman 2013) and securing suitable measurements over time scales of years remains a valuable area for research to understand the factors determining the structure and dynamics of coral bommies.

By addressing aspects of patch formation in the back reef of Moorea, our study explores factors contributing to the shape and size of bommies, which influences how these small habitat fragments might mediate reef-wide diversity and ecological resilience (Rietkerk et al. 2021, Szangolies et al. 2022). We conclude that coral bommies in the lagoon of Moorea better reflect legacy accretion than contemporary accretion. Coral community in the lagoon of Moorea may already be so depleted in abundance of reef-building species (like massive *Porites* spp.) that it will be challenging for contemporary accretion or fragmentation to alleviate biodiversity loss or reduced community resilience (sensu Rietkerk et al. 2021).

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