Plasticity in Three-Dimensional Geometry of Branching Corals Along a Cross-Shelf Gradient

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Abstract: Scleractinian corals often exhibit high levels of morphological plasticity, which is potentially important in enabling individual species to occupy benthic spaces across a wide range of environmental gradients. This study tested for differences in the three-dimensional (3D) geometry of three branching corals, *Acropora nasuta*, *Pocillopora* spp. and *Stylophora pistillata* among inner-, mid- and outer-shelf reefs in the central Great Barrier Reef, Australia. Important attributes of coral morphology (e.g., surface area to volume ratio) were expected to vary linearly across the shelf in accordance with marked gradients in environmental conditions, but instead, we detected non-linear trends in the colony structure of *A. nasuta* and *Pocillopora* spp. The surface area to volume ratio of both *A. nasuta* and *Pocillopora* spp. was highest at mid-shelf locations, (reflecting higher colony complexity) and was significantly lower at both inner-shelf and outer-shelf reefs. The branching structure of these corals was also far more tightly packed at inner-shelf and outer-shelf reefs, compared to mid-shelf reefs. Apparent declines in complexity and inter-branch spacing at inner and outer-shelf reefs (compared to conspecifics from mid-shelf reefs) may reflect changes driven by gradients of sedimentation and hydrodynamics. The generality and explanations of observed patterns warrant further investigation, which is very feasible using the 3D-photogrammetry techniques used in this study.

Keywords: coral reefs; growth; morphology; function; photogrammetry; surface area; traits; volume

1. Introduction

Variability in traits is known to influence species' functional importance in ecosystems [1]. Trait plasticity among individuals of the same species constitutes a major component of this variation [2], however intraspecific variability is often ignored due to difficulties in measuring the traits of individuals at large scales and with readily quantifiable metrics. On tropical coral reefs, morphological variation among reef-building corals is a conspicuous and functionally important source of trait variation. Coral morphology is associated with critical attributes including growth [3], photosynthesis [4], fecundity [5], susceptibility to disturbance [6] and life history [7]. The structural complexity, surface area and hole size of corals can also influence the diversity and abundance of associated reef fish species [8,9]. It is not surprising, therefore, that previous measures of trait diversity in corals are heavily focused on among-species differences in morphology [10,11]. Nevertheless, our understanding of morphological plasticity within species is still emerging, putting into question

the true extent of inter-specific differences and the capacity for corals to modify their functional attributes in response to changing environmental conditions [12].

Morphological plasticity in scleractinian corals can be substantial [12] and is most often linked to variation in light and/or water flow [13–15]. Marked inter- and intra-specific differences in the growth and morphology of scleractinian corals have been documented with depth, which is generally attributed to changing light conditions (e.g., references [14,16,17]). Anthony et al. [16] showed that variation in the morphology of *Turbinaria mesenterina* optimizes within-colony irradiance along gradients of depth and light, shifting from tightly spaced whorls in shallow, high light environments to horizontal plates in deeper, low light environments. Changes to coral morphology can also occur in response to water flow. In Hawaii, Lesser et al. [18] observed that *Pocillopora damicornis* collected from high flow environments had thicker branches, compared to conspecifics from low flow environments, which is likely to increase resistance to more extreme flow conditions. Importantly, erect branching corals are extremely vulnerable to breakage and dislodgement from large storm-generated waves [19]. Morphological plasticity may allow coral species to tolerate a much wider range of environmental conditions and thereby greatly extend their capacity to occupy different environments. There are however few efficient, universal, quantifiable measures of morphology and the mechanistic drivers of this variation are yet to be explored.

Although not tested, coral morphology is also likely to vary along cross-shelf (inshore to offshore) gradients, reflecting changes in sediment loads [20], light penetration [21,22], input of terrestrial nutrients [23], and wave exposure [24]. Such differences in colony morphology may in turn influence the functional role of corals (e.g., influencing occupation by coral-dwelling fishes [25]) as well as their vulnerability to disturbance (e.g., reference [19]). While there are conspicuous cross-shelf differences in the species composition of coral assemblages and relative abundance of different corals (e.g., references [26,27]), some coral species do occur across inner-, mid- and outer-shelf reefs (e.g., reference [28]). Corals living on outer-reefs are likely to experience much higher wave exposure and water movement [24], whereas corals in inner-shelf reefs will be much more exposed to land-based sources of nutrients, sediments and pollutants [29,30]. As such, we would expect that corals would be more compact in response to increasing mechanical exposure, from inshore to offshore [31,32]. Conversely, corals from inner-shelf, near shore environments might be expected to have more simple structures and lower surface area compared to conspecifics from outer-shelf reefs, reflecting increased reliance on heterotrophy and greater capacity for sediment shedding [13,22,33].

This study explores variation in the three-dimensional structure of three species of coral, *Acropora nasuta*, *Pocillopora* spp. and *Stylophora pistillata* among inner–, mid– and outer-shelf reefs in the central Great Barrier Reef (GBR), Australia. Specifically, this study tests two potentially competing hypotheses regarding cross-shelf variation in colony structure. Notably, increasing mechanical exposure at offshore reefs may lead to more compact or robust morphologies, but also high levels of sedimentation and turbidity in near shore environments may lead to reduced complexity and surface area of coral colonies. This study is novel because rather than using standard morphometric measurements, variation in colony structure is discerned using high resolution 3D photogrammetric modeling (e.g., references [34,35]) with novel metrics used to characterize important attributes of colony structure. This study will further highlight how 3D photogrammetric modeling can be applied to examine the biology and ecology of scleractinian corals. Importantly, differences in colony structure may have important effects on demography and population dynamics in different habitats [19,28] as well as influencing key ecological functions (e.g. predation [36], physical refuge and spatial competition [2,37]) of branching corals [25,38].

2. Materials and Methods

2.1. Sample Size and Collection

Replicate coral colonies of each of three different coral species (*Acropora nasuta*, *Pocillopora* spp., and *Stylophora pistillata*) were collected during December 2016 at six reefs in the central GBR deemed representative of inner-shelf (Pelorus and Orpheus), mid-shelf (Bramble and Truck) and outer-shelf (Pith and Unnamed) locations. All sampling was conducted on the western margin of each reef, to standardize local exposure to south-easterly swells, although there are still expected to be increases in wave exposure and water movement with distance offshore [24]. Corals used in this study were collected primarily to test for cross-shelf variation in coral growth using staining [28]. Inherent differences in coral abundance and survival of stained colonies led to uneven sampling among locations; a total of 96 corals were successfully collected, bleached, transported to Townsville and imaged for photogrammetry (Table 1). Most notably, samples of *S. pistillata* at inner-shelf or mid-shelf reefs were very limited, due to low abundance and poor survival of these corals, respectively [28]. These data are nonetheless included, to test for intra-specific variation in colony attributes.

Table 1. Summary of coral colonies of each species sampled from each location in this study.

Species	Inner-Shelf	Mid-Shelf	Outer-Shelf
Acropora nasuta	16	4	12
Pocillopora spp	18	17	16
Stylophora pistillata	1	0	10

2.2. Photogrammetry & Measurements of Complexity

This study was opportunistic, making use of coral skeletons where coral colonies were collected and sacrificed to document growth rates [28]. All colonies were therefore, imaged under lab conditions. Individual coral colonies were oriented as they grew naturally on a table and imaged in air using a Cannon Powershot Gx7 handheld camera ('Auto' setting, 9 mm focal length, 20MP, 5472 × 3648), with two scale features (Rubik's Cubes and set squares) of known size (55 mm and 127 mm respectively) included in the scene. Image capture followed a hemispherical pattern as described in Figueira et al. [34], providing approximately 100 images captured from various angles with >80% overlap amongst adjacent images. Images were taken from similar distances (~500 mm) to the colony however, where necessary, the distance of the camera was adjusted to ensure that the colony remained the dominant feature of each image.

Three-dimensional (3D) models of each colony were built using the software Photoscan Professional (V1.4.1, Agisoft LLC, St. Petersburg, Russia) as per Ferrari et al. [35]. Images were initially filtered for suitability using the "Estimate Image Quality" tool with low quality images (typically quality value < 0.5) removed from consideration. Model building generally followed the standard photogrammetry methodology (see Table 2 for parameter values) though the dense cloud was trimmed to include just the coral model prior to building of the mesh. The model was scaled at the dense cloud stage using two separate objects of known size (Rubik Cube, 55 mm), one in the horizontal and one in the vertical dimension.

Once complete, coral meshes were exported from Photoscan Professional (V1.4.1, Agisoft LLC, St. Petersburg, Russia) and imported to GeoMagic Control (V2015, 3D Systems, Rock Hill, USA). Self-intersections, non-manifold edges, small holes and small features were eliminated via the 'Mesh Doctor' function then surface area and volume measurements were taken and the ratio of surface area to volume (SAV) was calculated. ArcScene (V10.5, ESRI. Redlands, USA) was used to construct and measure the volume of a 3D minimum bounding convex hull (Figure 1). From this the proportion occupied (Coral Volume/Convex Hull Volume) was calculated. High proportion occupied (PrOcc)

ratios indicates less free space between coral branches, which suggests a more compact or club-like growth structure.

Table 2. Summary of parameters (from Agisoft Photoscan Professional, V1.4.1, St. Petersburg, Russia) used to construct 3D models of corals in this study.

Process	Settings
Photo alignment	High accuracy, pair and reference preselection disabled, key point limit 40,000, tie point limit 4000, features not constrained by mask, no adaptive camera model fitting
Sparse point cloud	All optimisation properties 'yes' except fit b1, b2, k4, p3, p4, adaptive camera model fitting
Dense point cloud	High quality *, moderate depth filtering, do not reuse depth maps, calculate point colors
Mesh	Arbitrary surface type, source data-dense cloud, face count high, interpolation enabled, all point classes, don't reuse depth maps
Texture	Generic mapping mode, texture from all cameras, mosaic blending mode, texture size 8192, texture count 1, hole filling

* Ultra high dense cloud was used in a few cases where Photoscan assigned a disproportionate number of points to the periphery of the model such that a model of equivalent resolution was obtained.
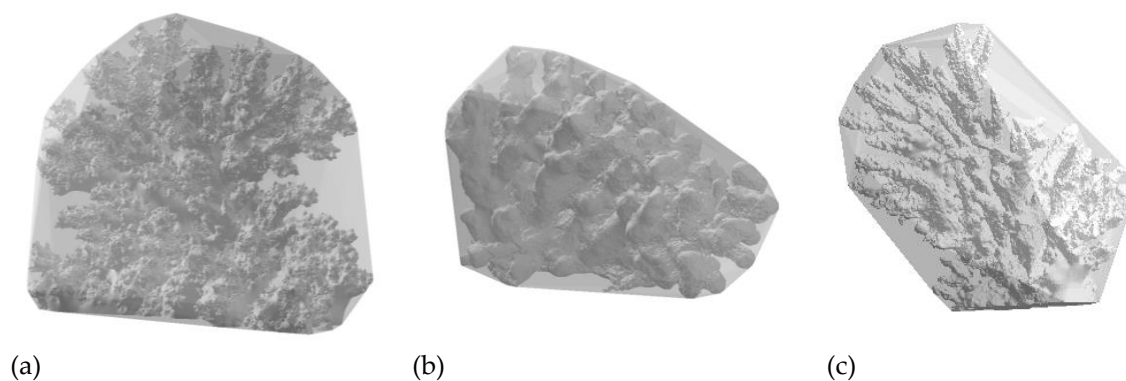

(a)　　　　　　　　　　　　　　(b)　　　　　　　　　　　　　　(c)

Figure 1. 2D views of representative colonies of (**a**) *Pocillopora spp.* (**b**) *S. pistillata* and (**c**) *A. nasuta*, each encased by minimum bounding convex hull. Note that metrics were derived in 3D.

2.3. Statistical Analysis

General Linear Models (GLM) were used to evaluate the effect of Shelf Position (fixed, three levels) and Species (fixed, two levels) on the two metrics of structural complexity considered here, PrOcc and SAV. Reef was included as a random nested factor within Shelf Position. Samples ranged in physical size (here expressed in 'bounding volume') from 0.155×10^3–4.702×10^3 m^3. To control for the possibility that the interior regions of larger corals may be more poorly resolved (leading to overestimated PrOcc and underestimated SAV values) as they are not as clearly visualized by photographs, we included the volume of the minimum convex hull as a covariate in the statistical model. This is also appropriate to deal with the known relationship between colony size and SAV. Normality was assessed using Shapiro-Wilks with SAV data requiring a logarithmic transformation. Homogeneity of variance was evaluated using Cochran C tests with no transformations required. Tukey's Post Hoc analyses were used to assess differences amongst treatment groups as needed. All analyses were conducted in Statistica (V12, TIBCO Software Inc., Palo Alto, USA). *Stylophora pistillata* was excluded from statistical analyses due to low samples sizes at inshore and mid-shelf locations (Table 1), though results are displayed graphically for comparison.

3. Results

3.1. Proportion Occupied (PrOcc)

The GLM indicated that the proportion of 3D space occupied (PrOcc) was significantly higher in *Pocillopora* spp. than *A. nasuta* (significant effect of Species; $F_{1,73}$ = 10.89, p = 0.001; Figure 2a; Figure 3) and that this was consistent among shelf locations (no Shelf Position*Species interaction; $F_{2,73}$ = 2.10, p = 0.13). Despite this, the individual colony minimum PrOcc for *Pocillopora* spp. (Mid-shelf; 16.8%) was lower than that of *A. nasuta* (Inshore; 18.2%) while the maximum value was higher in *Pocillopora* spp. (Inshore; 59.8%) compared to *A. nasuta* (Inshore; 53.6%), indicating a greater overall range of PrOcc values among *Pocillopora* spp. colonies. Offshore *S. pistillata*, colonies proved to have the highest PrOcc, and therefore most compact growth forms, of all spices considered here while at inshore sites they had the lowest values observed. There were significant differences in PrOcc amongst Shelf Positions ($F_{2,73}$ = 12.82, p = 0.014) with post-hoc tests indicating that inshore colonies of both species had higher PrOcc values than either mid-shelf ($p < 0.001$) or offshore (p = 0.017) colonies. While there was a trend for PrOcc values to be higher in the offshore than midshelf region, this was not statistically significant (p = 0.07; Figure 3). There was no effect of Site[Shelf Position] ($F_{1,73}$ = 0.80, p = 0.495) or colony size ($F_{1,73}$ = 0.82, p = 0.369) on PrOcc values.
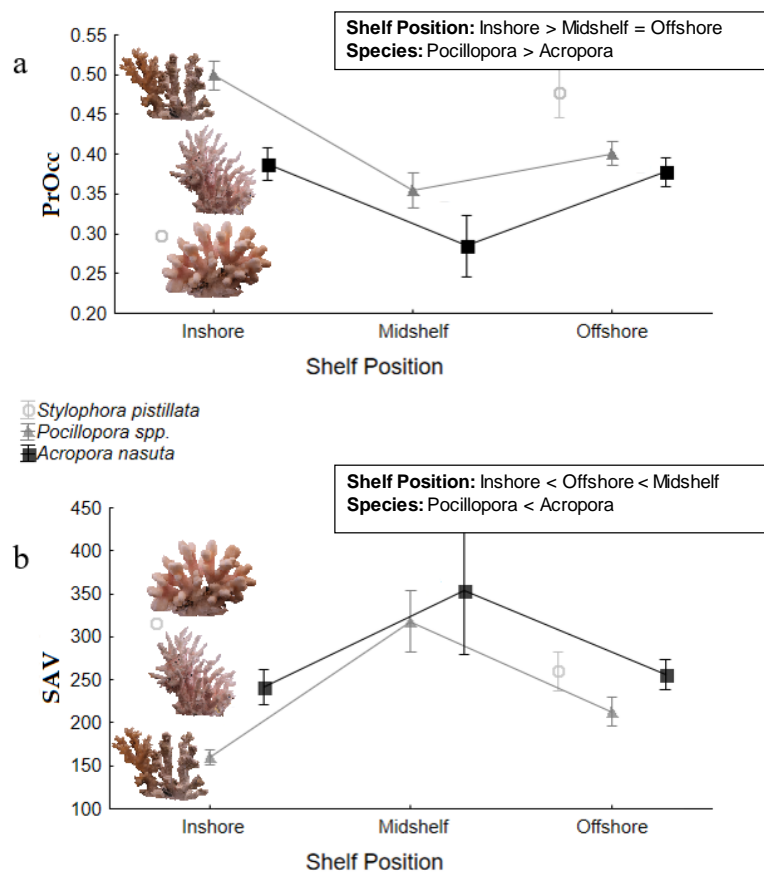

Figure 2. Mean (±SE) values for each metric of structural complexity derived from 3D models of colonies of each species evaluated in this study; (**a**) proportion of minimum convex hull occupied (PrOcc) and (**b**) surface area to volume ratio (SAV). Results for Shelf Position and Species groups are shown; there was no interaction between these two factors. Factor-level comparisons based on post-hoc tests are given in the inset boxes for reference. Data for *Stylophora* is also included for reference but was not tested statistically due to low sample sizes.
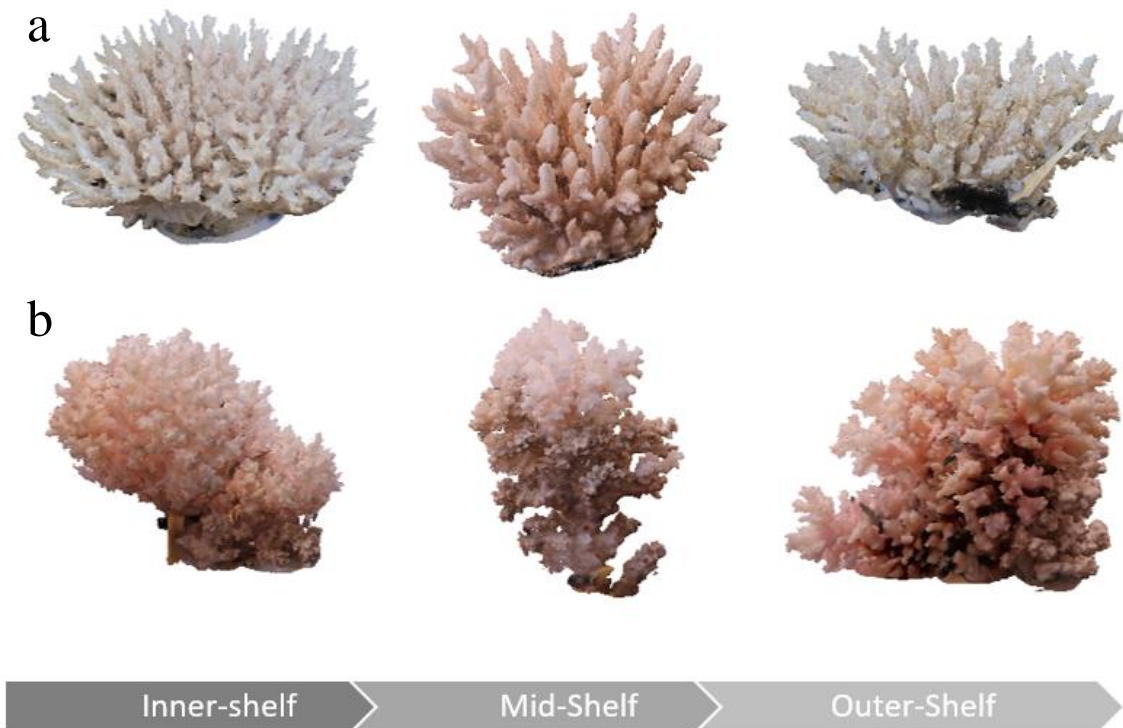
a

b

Inner-shelf 〉 Mid-Shelf 〉 Outer-Shelf

Figure 3. Representative examples of variation in colonies of *A. nasuta* (**a**) and *Pocillopora spp.* (**b**) along the cross shelf gradient.

3.2. Surface Area: Volume Ratio (SAV)

The GLM indicated that the SAV of *A. nasuta* was significantly higher than that of *Pocillopora* spp. ($F_{1,73}$ = 6.08, *p* = 0.016), a pattern which was consistent across all shelf positions (no Shelf Position*Species interaction; $F_{2,73}$ = 1.50, *p* = 0.229; Figure 2b; Figure 3). Nevertheless, *Pocillopora* spp. proved to have the greatest range in SAV of the species tested, with an inner-shelf colony and mid-shelf colony showing the lowest (111.4) and highest (653.8) SAV respectively (Figure 3). SAV for *S. pistillata* tended to be most similar to *A. nasuta*, with a greater SAV than *Pocillopora* spp. however as no statistical tests were applied, we cannot determine if this difference was significant. There was a significant effect of the Shelf Position on the SAV of colonies ($F_{2,73}$ = 11.45, *p* = 0.012). Post-hoc tests indicated that the SAV of inner-shelf colonies (*Pocillopora* spp.: 159.9; *A. nasuta*: 240.9) were significantly lower than mid-shelf (*p* < 0.001; *Pocillopora* spp.: 318.0; *A. nasuta*: 353.4) and outer-shelf (*p* = 0.015; *Pocillopora* spp.: 213.1; *A. nasuta*: 256.2) colonies, and that outer-shelf values were significantly lower than the mid-shelf (*p* < 0.001). Consequently, mid-shelf colonies had the greatest SAV and this pattern was consistent across both species. There was no effect of Site[Shelf Position] ($F_{1,73}$ = 0.58, *p* = 0.627) however the co-variate for colony size (Bvol) was significant ($F_{1,73}$ = 56.35, *p* < 0.001), a pattern that was expected due to the known relationship between surface area and size.

4. Discussion

High resolution 3D photogrammetric modelling is greatly enhancing the study and understanding of morphological variation in scleractinian corals [34,35]. In this study, 3D photogrammetric modeling, combined with novel metrics of colony attributes, revealed non-linear changes in the structure across a cross-shelf gradient. Notably, the SAV of both these species was highest at mid-shelf locations, (reflecting higher colony complexity) and was much lower at both inner-shelf and outer-shelf reefs (Figure 2b). Similarly, colonies of both *Pocillopora* spp. and *A. nasuta* were much more open (or less compact) at mid-shelf reefs, based on higher levels of PrOcc at both inner-shelf and outer-shelf reefs.

These non-linear relationships may reflect synergistic outcomes of cross shelf gradients with opposing effects on the structure of coral colonies.

Near shore marine environments are increasingly impacted by anthropogenic modification of coastal and catchment systems, resulting in widespread transformation and degradation of marine habitats [39–41]. For inner-shelf reefs, high levels of suspended sediments, nutrients and pollutants have resulted in localized coral loss in some cases [39,42,43], though direct effects of these environmental stressors on coral morphology are largely unknown. In this study, colonies of both *Pocillopora* spp. and *A. nasuta* were less complex (lower SAV) with more tightly packed (or possibly thicker) branches (higher PrOcc) at inner-shelf reefs compared to mid-shelf reefs, which may reflect morphological adaptations to higher sedimentation, nutrients and reduced light availability [22,44]. We did not however, explicitly measure the environmental conditions at individual study locations, and the specific drivers of observed differences will need to be investigated experimentally. This trend also does not continue universally across the shelf gradient, with a drop in SAV and increase in PrOcc at offshore sites compared to mid-shelf. It has been suggested, that even for mid-shelf morphs of some branching species (*Pocillopora damicornis* and *Acropora milepora*), sediment shedding ability is greater than any natural nearshore sedimentation rate, even when tested in static flow [45]. It is therefore possible that morphology of nearshore colonies examined in this paper are not significantly affected by a need to shed terrestrial sediments; but may be more closely linked with other factors such as nutrient availability, light and active predation [46,47]. Porter et al. [48] hypothesized that interspecies morphs with lower SAV would have a greater propensity for heterotrophic feeding as opposed to more photic-reliant branching (high SAV) morphs. Interspecific variation was found between feeding activity in branching (high SAV) and mound (low SAV) species with high feeding activity in those with low SAV. Similarly, intraspecific plasticity in feeding behavior with depth, and therefore possibly light, was found in some species, including *P. damicornis* [13,44].

Erect, branching corals are extremely vulnerable to hydrodynamic forces generated by large waves [49,50] which accounts for changes in morphological structure along gradients of mechanical exposure [18]. Most notably, corals are expected to have thicker, stronger branches in high energy environments [18], which may be consistent with observed increases in PrOcc between mid-shelf and outer-shelf reefs for both *Pocillopora* spp. and *A. nasuta.* Colonies of these corals also had lower complexity (lower SAV) at outer- versus mid-shelf reefs, however higher complexity was shown (higher SAV) at outer- versus inner-shelf reefs. High PrOcc coupled with low SAV may suggest thicker branches while the same PrOcc and high SAV would more likely suggest smaller tightly packed branches. These results indicate the possibility in this study of thicker branches at inner- compared to outer-shelf reefs, which is contrary to the majority of the literature [18,44,51].

As a sister study to a growth rate experiment [28], collection of corals used in this paper were limited to the methodologies required to measure growth. This resulted in a very small sample of *S. pistillata* and a reduced number of mid-shelf *A. nasuta* samples (Table 1). Relatively high variance was observed in SAV for mid-shelf *A. nasuta*. While SAV for these samples ranged from 237.5–551.4, there were no distinct outliers with samples spread evenly across this range. Despite the relatively high variance, significance was still detected, highlighting the large effect size at this shelf position.

The non-linear variation in the 3D structure of corals along cross-shelf gradients in this study is best explained by considering synergistic effects of different environmental factors, which lead to lower complexity and more tightly packed or thicker branches at inner- versus outer-shelf reefs. It is, however, also possible that these patterns reflect non-linear changes in environmental conditions. Nutrient concentrations, for example may be higher on inner- and outer shelf reefs, compared to mid-shelf reefs, albeit for very different reasons [46]. As discussed in Wolanski et al. [52], complex hydrodynamic forces may be responsible for nutrient upwelling at off shore sites. This would decrease the need for autotrophy allowing for offshore morphs to have similar characteristics to nearshore colonies [46]. Despite this, upwelling has also been shown to limit active predation rates in *P. damicornis* either as a function of slowed polyp reaction with reduced temperature, or higher nutrition per

zooplankton encounter [44]. Observed patterns of morphological variation may also be independent of environmental gradients. It is likely that over such a vast and abstract gradient, multiple cryptic drivers, including non-environmental ones, are interacting to produce the observed patterns. While morphological plasticity in response to local conditions is often regarded as a driver for within-species structural variation [53,54], increased awareness and ability to detect genetic divergence has allowed for cryptic species complexes to be identified [55,56]. Discovery of cryptic species complexes in scleractinian and gorgonian corals including *P. damicornis* and *Eunicea flexuosa* hint at potentially less flexible phenotypes coupled with independent evolutionary lineages in some species where plasticity has previously been suggested [55,56]. Indeed, in this study, *P. damicornis* (heralded as a prime example of morphological plasticity) was labeled *Pocillopora* spp., as we could not 100% guarantee the species identity of all samples. It is possible therefore that observed variation in morphology is not primarily driven by plastic responses to environmental gradients [14].

Morphological variation among scleractinian corals is a functionally-important component of coral reef trait diversity [57] which accounts for many ecological and macroevolutionary differences among species. However, rigorous measurements and readily quantifiable measures of coral morphology are lacking [5,57]. In this study, we show that 3D photogrammetry provides an extremely practical and tractable method for quantifying coral morphology. Importantly, the surface area to volume ratio, which has been proposed as a highly informative trait for scleractinian corals [57], can be readily calculated from 3D reconstructions of individual colonies and captures both inter- and intra-specific variation in colony morphology. We have shown that photogrammetric methods and novel proxies relating to structure are able to identify intraspecific changes in coral colony morphology. The pattern observed using these high-resolution metrics—increased structural complexity and openness of corals on the mid-shelf as opposed to in- and off-shore areas—is intriguing and suggests an interacting role of nearshore terrestrial run-off and offshore wave energy. Such dynamics may also be important in explaining patterns of other coral species across shelf gradients, as well as the ultimate drivers of trait variation within different groups of benthic organisms.

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