Colony compactness predicts growth and survival in corals

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Abstract

Understanding differences in growth and survival rates across species is a key element of anticipating how ecosystems are likely to respond to global change. However, measuring vital rates for highly diverse assemblages with many rare species is often unfeasible. Identifying links between traits and vital rates that apply across entire groups of species can provide a way to infer assemblage-wide demographic variation at the same time as identifying how traits relate to life history strategies. We combined 3D models of coral colonies with field measured vital rates to explore how mortality and growth vary with colony size and three morphological traits: sphericity, convexity and surface area to volume ratio. We showed that sphericity is negatively related to size-specific mortality and positively related to variation in net growth across a representative range of colony shapes. Further, sphericity significantly modulates size-demography relationships as colony size increases. Sphericity consistently outperformed surface area to volume ratio, highlighting that morphological compactness is a key driver of life history strategies that is independent of colony size. These results suggest that variation in colony compactness in an important axis of demographic strategy differentiation in corals.

Keywords

Reef coral, morphology, growth, mortality, survival, life history, laser scanning,

Introduction

How fast an organism grows and how long it is likely to live is highly variable even within closely related taxa. Life histories distribute along a fast-slow gradient: at one extreme, there are live-fast-die-young strategies; at the other extreme, there are slow-and-steady strategies, where an organism matures and grows over an extended period of time, but has a lengthy reproductive phase with low mortality risk (Stearns, 2000, 1976). This variation in demographic strategies has implications for organisms' contribution to ecosystem function, where growth rates determine contributions to production, while survival rates determine biomass production, and for ecosystem engineers, stability of habitat structure. However, whilst measuring demography for each species in low diversity assemblages is possible, for assemblages with high diversity an inordinate amount of research effort is required (Madin et al., 2016). Moreover, because most species in any assemblage are rare (McGill et al., 2007), estimates of demographic rates for these species have inherently high uncertainty. Identifying functional traits that are measurable and linked to organism performance can facilitate predicting assemblage dynamics independently of taxonomic identity (Cadotte et al., 2015; McGill et al., 2006). Here, we ask if geometric descriptors of coral shapes can be used as functional traits.

The development of trait based ecology (McGill et al., 2006; Violle et al., 2007) has led to the proliferation of trait measurements and compilations such as TRY for plants, AVONET for birds, and The Coral Traits Database for corals (Kattge et al., 2011; Madin et al., 2016; Tobias et al., 2022). However, not all traits that can be measured are informative, justifying the need to identify which traits are functional traits. The definition of "functional traits" is controversial (McGill et al., 2006; Violle et al., 2007) with recent calls to abandon the term completely in favour of working backwards from the (ecosystem) function of interest to traits that can predict these functions (Streit and Bellwood, 2023). Growth and survival in reef-building corals are not only fundamental measures of organism performance, they are also directly linked to ecosystem function through the accretion of reef superstructure and structural complexity (Baird and Marshall, 2002; Graham and Nash, 2013). Previous work has outlined how coral morphology can unify organism performance, ecosystem function, and response to changing environments (Zawada et al., 2019b). Here, we test three morphological traits and their capacity to explain variation in growth and survival across a broad range of colony shapes and sizes.

There is a large body of evidence suggesting coral morphology is linked to demography (Álvarez-Noriega et al., 2016; Baird and Marshall, 2002; Chappell, 1980; Darling et al., 2012; Dornelas et al., 2017; Highsmith, 1982; Madin et al., 2014). Typically, demographic variation is identified as differences between growth forms modulated by variation in colony size. For example, boulder-like massive colonies have been shown to have distinct size-mortality curves compared to open-branching colonies (Madin and Connolly, 2006; Massel and Done, 1993). In another example, year-to-year net growth was shown to be more variable in branching growth forms (Dornelas et al., 2017). These growth form-size-demography relationships work well to describe *what* is different between these groups, but they cannot be used to explain *why* variation in shape correlates with variation in demography.

Measuring quantitative morphological traits that co-vary with demography across a broad range of growth forms would allow demographic rates to be inferred for other colonies and species.

The varied and complex shapes of coral colonies have driven the reliance on growth forms as categorical idealizations of what is in reality continuous variation in shape. To uncover generalisable trait-demography relationships, continuous quantitative traits need to be identified. Relevant candidates include surface area to volume ratios (SA:Vol) (Chappell, 1980; Reichert et al., 2016; Vollmer and Edmunds, 2000), space filling dimension (George et al., 2021), interstitial space volume (Million et al., 2021), and shelter volume (Urbina-Barreto et al., 2021). However, many of these variables conflate shape and size effects, or are related more to ecosystem function than organism performance. SA:Vol is likely to affect growth for energetic reasons because surface area is associated with how much live tissue a colony has and hence how much energy it has available from symbiotic algae as well as heterotrophic feeding. In contrast, volume is associated with how much skeleton has been deposited. Therefore, more net energy-generating tissue (SA) per unit of net energy-costing structure (Vol) is likely to lead to faster growth rates. Yet, a limitation of SA:Vol as is that it conflates shape and size information. In the extreme, this means that a very small boulder colony could have the same SA:Vol as a larger branching colony, despite pronounced differences in their size, shape, or function. The interdependence of SA:Vol on size makes uncovering causal demographic links difficult. For example, is a positive association between SA:Vol and growth driven by size, shape, or their interaction? Including both size and SA:Vol in a model can alleviate this somewhat, but the inescapable collinearity between them will likely obfuscate the underlying relationships between size and shape. Another approach would be to use shape variables that are size independent, allowing their effects on vital rates to be partitioned.

Coral growth forms are distributed along three main axes of shape variation and occupy continuous morphological trait space defined by quantitative, size-independent shape variables (Zawada et al., 2019a). Volume compactness captures the sturdiness of colonies from compact boulder colonies to intricate and more fragile branching colonies. Volume compactness can be measured by two shape variables: sphericity and convexity. Volume compactness should be linked to whole-colony mortality and growth because this trait ultimately captures how surface area and volume are distributed. High sphericity colonies (i.e., more boulder-like) will necessarily have to precipitate a high volume of mostly inert skeleton for little living surface. This means that they will--given similar growing conditions--grow slowly compared to low sphericity (i.e. branching) colonies. However, the structural integrity high sphericity affords makes them much less likely to break or dislodge compared to branching colonies. Previous work on growth forms suggests that low-compactness growth forms are more likely to dislodge (Madin and Connolly, 2006), have a higher susceptibility to disease (Palmer et al., 2010), are more resilient to bleaching (Kaniewska et al., 2008), and are preferentially predated upon by crown of thorns starfish (De'ath and Moran, 1998). Growth forms with high compactness show slower net growth rates compared to branching colonies (Dornelas et al., 2017; Gladfelter et al., 1978). However,

whilst branching colonies can grow faster, they are more likely to partially break (Lirman, 2000; Madin et al. 2020). Consequently, a low-compactness colony is likely to have a high growth variation; one year a colony can increase in size significantly, whilst decreasing in size the next year. Taken together, volume compactness may capture a gradient in demographic strategy from slow-and-steady to boom-and-bust that partially contributes to the high diversity of coral assemblages.

The aim of this study was to determine how much volume compactness may explain the variation in size-demography relationships among different growth forms of corals, expressing the relationship between demography and morphology along a common set of axes. First, we asked: (1) Can we predict morphological traits from colony size and growth form? (2) Do morphological traits improve on the explanatory power of size-demography relationships? (3) Can morphological traits and colony size be used to predict growth and mortality for other growth forms? We hypothesise that volume compactness will be positively correlated with survival due to higher structural integrity, negatively correlated with net growth due to skeletal bulk growth outpacing living surface capacity, and negatively correlated with year-to-year growth variation due to the tension between slower growth yet resistance to partial mortality.

Methods

Predicting morphological traits using colony size and growth form

152 coral skeletons were laser scanned, capturing 10 growth forms and three orders of magnitude in size (Zawada et al. 2018). For each resulting 3D mesh, we calculated planar area, surface area to volume ratio (SA:Vol) and two measures of volume compactness from Zawada et al. (2018): sphericity and convexity. For each growth form, we then fitted linear models for each morphological trait (SA:Vol, sphericity and convexity) as a function of planar area. Sphericity and convexity are bounded by 0 and 1, and so were logit-transformed before analysis. To assess the suitability of each growth form and morphological trait model, we ran a leave-one-out analysis for each observation and calculated the average mean absolute error (MAE). Models were compared to an intercept-only model and the best performing model for each shape variable and growth form combination was retained (Table S1).

Using morphological traits to improve demographic estimates

Yearly growth and survival rates were estimated from a long-term demography study at Lizard Island in the northern Great Barrier Reef (Madin et al. 2023). From 2009 to 2014, thirty colonies each from 11 species representing five growth forms were tagged. The five growth form categories were: arborescent (*Acropora intermedia, A. robusta*), corymbose (*A. spathulata, A. nasuta, A. millepora)*, tabular (*A. hyacynthus, A. cytherea)*, digitate (*A.* aff *digitifera, A. humilis)*, and massive (*Goniastrea retiformis, G. pectinata*). If one of the 330 colonies died, went missing, or could not be located between years, additional colonies were tagged to keep the number of replicates at thirty per species for each year. No cyclones or mass bleaching events were recorded during the survey years, and while *Acanthaster planci* were present in

some years, the mortality caused by this coral predator was low at the study site (Madin et al. 2018)

Growth was calculated as net change in planar area, where colonies could grow, shrink, or remain the same size between years due to the combination of growth and partial mortality (Dornelas et al. 2017). To measure growth, colonies were photographed with a scale plate from above each year and photos were corrected for barrel distortion. Photos were used to calculate planar area, a 2D measure of colony size. Changes in size were calculated for each year from 2009 to 2014. Mortality was a binary variable denoting whether the colony was alive or dead based on the *in situ* surveys of tagged colonies. Colony mortality was tracked each year from 2009 to 2014, where colonies were marked as alive, dead, or missing if the tagged colony could not be located. Morphological traits (SA:Vol, sphericity, and convexity) were estimated for each field colony based on their planar area and growth form using the predictive shape-variable regression models. We filtered the demography dataset such that each growth form had a similar size range as the focus of this study was to assess how shape modulates size-demography relationships across growth forms.

We used the *gamlss* package (Stasinopoulos and Rigby, 2007) for R (R Core Team, 2015) to model all vital rates as functions of colony morphological traits and size. *gamlss* allows the standard deviation to be an estimated parameter in addition to the mean to allow predictors of variation in growth in addition to net growth. Net growth was modelled using a gaussian distribution and mortality was modelled using a logit distribution specified within *gamlss*. We used BIC, AICc and explained deviance (R^2) to compare models. R^2 was calculated following Nagelkerke (1991) using the Cox & Snell method. Size interacting with shape and fixed effects only models as well as intercept only-models were fitted for each shape variable with the selected model by BIC presented here. We then compared BIC, AICc, and R^2 values for the selected models for each shape predictor to determine which predictors best explained variation for each vital rate, focussing on BIC.

We used a two-step approach for the growth models to allow for model selection for both the mean and standard deviation components of growth separately. First, we selected the mean net growth model with the lowest BIC. We then used the residuals from this model as the response in the standard deviation model, where the residuals represent the remaining variation after removing the net growth model estimates. This allowed us to apply model selection on mean net growth and growth variation sequentially.

Predicting demography for growth forms using morphological traits

To test the predictive power of the demography models we applied a leave-one-growth-form out analysis, where the size-only and selected morphological trait models were re-fit leaving one growth form out at a time, with between 150 to 261 points left out depending on growth form. This model was then used to predict growth and mortality for the remaining data. Aggregated predicted performance for both models was then compared to aggregated observed demographic values.

Mortality was assessed by comparing the mean predicted probability of mortality and the mean observed mortality for all observations. Net growth was assessed by comparing the mean predicted net growth and observed mean net growth across observations. Growth variability was assessed by comparing the mean of the predicted standard deviation and the observed standard deviation in net growth across observations.

Results

Predicting morphological traits using colony size and growth form

All shape variables were well predicted for all growth forms (figure 1, table S1). For convexity, the arborescent colonies had the lowest mean absolute error (MAE: 0.197) followed by the tabular, digitate, corymbose, and finally the massive colonies (MAE: 0.396). For sphericity, the arborescent colonies had the lowest mean absolute error (MAE: 0.109) followed by the digitate, corymbose, tabular and finally the massive colonies (MAE: 0.334). For surface area to volume ratio (SA:Vol), the massive colonies had the lowest mean absolute error (MAE: 0.045) followed by the arborescent, digitate, tabular and finally the corymbose colonies (MAE: 0.113).

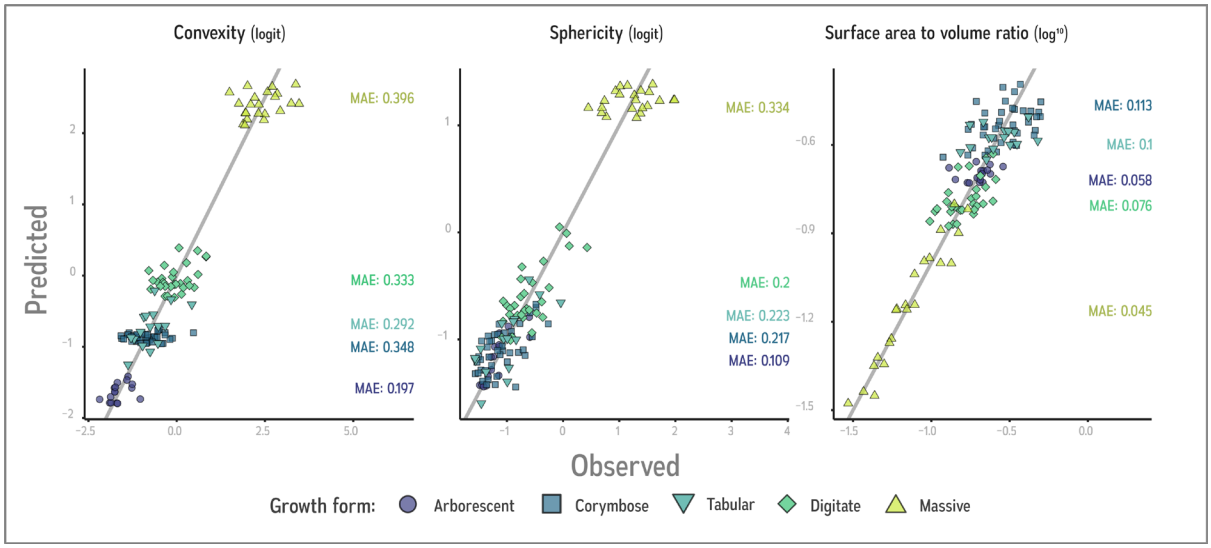


Figure 1. Predictive model performance for predicting convexity and sphericity (two measures of volume compactness) and surface area to volume ratios for five growth forms using planar area (the 2D area of a colony when viewed from above). Data for models come from high-resolution 3D laser scans of coral colonies. Predicted values generated using a leave-one-out approach. Aggregated predictive model performance metrics are calculated for each growth form and shape variable combination. MAE: mean absolute error. Grey line is the 1:1 line, with points exactly on the line indicating no error in prediction. Predictive model performance for all shape variable and growth form combinations is high, indicating that these models can be used to predict shape from growth form and size for other colonies.

Using morphological traits to improve size-demography models for growth and mortality

Mortality (figure 2, top row)

For mortality, the model with the lowest BIC was the size interacting with sphericity model (BIC: 654) which also had the lowest AICc (636) and highest pseudo R^2 (0.07). The model with the second lowest BIC was the size interacting with SA:Vol model (BIC: 662) which was 8 points higher suggesting that the size interacting with sphericity model was the most likely given the data compared to all other models. The size only model had the highest BIC (695) and AICc (685) and the lowest pseudo R^2 (0.007), suggesting that all models that included a shape variable component improved on the size-only model.

The size interacting with sphericity model for mortality (figure 2, A3) shows how sphericity modulates the size-mortality relationship. At small sizes all colonies, regardless of shape, experience high mortality which decreases as colony size increases. However, for colonies with very low sphericity and therefore more complex colony shapes, the rate of decline in mortality is slower, more linear and doesn't reach an asymptote over the size ranges in this study. As sphericity increases and colonies tend towards boulder-like, the size-mortality relationship becomes more quadratic, rapidly decreasing at smaller colony sizes and reaching an asymptote where mortality tends towards zero.

Similar, but less pronounced effects are found with the convexity (figure 2, A2) and surface area to volume ratio models (figure A4). Where more complex (low convexity/high surface area to volume ratio) colonies maintain higher mortality probability throughout their size range compared to more boulder-like forms. Interestingly, for convexity, the size-mortality relationship is quadratic and tends towards an asymptote across all quantiles over the colony size ranges in the analysis (figure, A1).

*Mean net growth (figure 2, middle row)*The model with the lowest BIC for mean net growth was the size only model (BIC: 15377). However, the model with the lowest AICc and the highest pseudo R^2 was the size interacting with sphericity model (AICc: 15358, pseudo R^2: 0.021), although this was closely followed by the size interacting with convexity model (AICc: 15359, pseudo R^2: 0.019). However, all size and shape models had BIC values 5 points or higher than the size-only model.

Net growth in the size interacting with sphericity model (figure 2, B3) captures a gradient of positive net growth, declining to negative as size increases for all sphericity quantiles except the 0.95 quantile, which sees slight negative growth at small sizes, becoming more positive as colony size increases. An almost identical pattern is seen for convexity (figure 2, B2). The surface area to volume ratio model (figure 2, B4) shows essentially no effect, with all quantiles starting at high net growth and declining towards negative as colony size increases. In addition, the SA:Vol model shows essentially the same trend as the size-only model (figure 2, B1).

Variation in net growth (figure 2, bottom row)

Using the residuals from the size-only net growth model (i.e. the one with lowest BIC), the model that best explained the data for growth variation was the size interacting with sphericity model (BIC: 13156). The size interacting with sphericity model also had the lowest AICc (13132) and highest pseudo R^2 (0.898). The size interacting with convexity model has the second lowest BIC (13172) and had the second lowest AICc (13147) and second highest pseudo R^2 (0.897). The size-only model had the highest BIC (13554), highest AICc (13540), and lowest pseudo R^2 (0.844).

The size interacting with sphericity model for net growth variation (figure 2, C3) shows how sphericity modulates the size-growth variation relationship. At small sizes all colonies, regardless of shape, have low growth variation that increases with colony size. However, for colonies with very low sphericity, growth variability rapidly increases with colony size where large, ornate colonies can either grow rapidly or shrink significantly between years. As sphericity increases colonies tend towards boulder-like, growth variation decreases for colonies of the same size. At the extreme high end of sphericity there appears to be no change in growth variation as colony size increases.

The size convexity model variation (figure 2, C2) shows almost identical relationship to sphericity, with constant variation at high convexity through to extreme growth or shrinkage at low convexity for large colonies. The SA:Vol model (figure 2, C4) differed dramatically in that it showed the reverse effect for colonies with extremely low surface area to volume ratios (i.e. the most boulder-like). In this case, large colonies with low surface area to volume ratios had the highest growth variation compared to colonies with higher surface area to volume ratios. All other quantiles for SA:Vol were clustered together with little change in the size-growth variation relationship from the 0.25 to 0.95 quantiles.

Predicting demography for growth forms using morphological traits

The size interacting with sphericity model was the size plus shape model with the lowest BIC for all three demographic parameters and was therefore chosen for the leave one growth form out analysis and contrasted with the size-only models.

For mortality (figure 3, top row), the size-only models performed poorly overall, with tabular and massive colonies being the most over and under-predicted respectively. Digitate and corymbose colonies were closer to the 1:1 line, and the arborescent colonies were very close, indicating strong predictive performance. The size and sphericity models performed better than the size-only models overall, with a large improvement in the massive colonies and a marginal improvement in the corymbose and digitate colonies. The arborescent colonies saw a minor improvement, but mortality was still largely overestimated by the model.

For net growth (figure 3, middle row), the size and sphericity model had a lower accuracy overall, with a large shift to overestimation in the tabular and massive growth form and shift to underestimation in the digitate and corymbose colonies.

For net growth variability (figure 3, bottom row), the size and sphericity model drastically improved on the size only model. Both tabular and arborescent growth forms were extremely overestimated in the size only model, and these growth forms were much closer to the 1:1 line in the size and sphericity models, with minor improvements to the corymbose colonies as well.

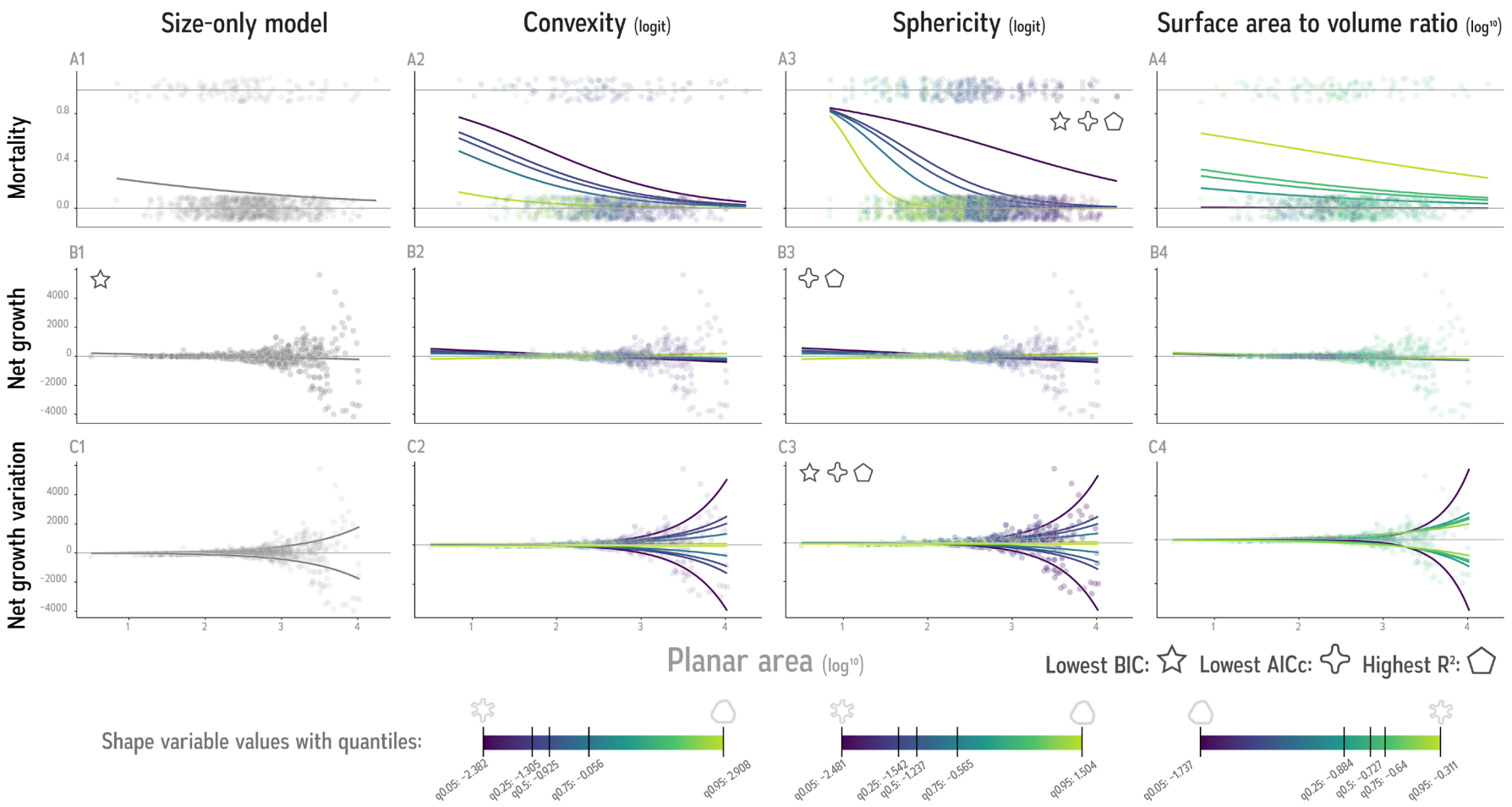


Figure 2. Data and model fits for explaining mortality, net growth, and growth variation using shape and size in reef-building corals. Response variables arranged from top to bottom. (top) logistic model fits for estimating whole colony mortality probability for a given year. (middle) gamlss model fits for estimating mean changes in net growth for a colony between years. Note the solid black line on zero, and how, for a given year, colonies may grow, shrink or stay the same size due to the counteracting effect of growth and partial mortality. (bottom) gamlss model fits for estimating in net growth variation (as standard deviation) for a colony between years. Response variable in these models are the residuals from the size-only mean net growth model. Again, note the solid black line at the zero net growth point. Explanatory variables arranged from left to right, with planar area on the x-axis and the response on the y-axis. (left) a model that only includes planar area as an

explanatory variable to be used as a point of comparison with size + shape models. (centre-left) The planar area interacting with sphericity models, where sphericity is a measure of volume compactness, broadly capturing a gradient from branching through to massive corals as sphericity increases. (centre-right) The planar area interacting with convexity models, where convexity is another measure of volume compactness complementary to sphericity, broadly capturing a gradient from branching through to massive corals as convexity increases. (right) The planar area interacting with surface area to volume ratio models, the surface area of the colony divided by its volume, capturing the relationship between biomass (surface area) and inert skeleton (volume). Planar area was measured *in situ*, shape variables were estimated from size and growth form models developed using high resolution 3D scans of coral skeletons (fig. 1). The size-only models are uncoloured, the size and shape models are coloured ranging from the minimum to maximum values for the given shape variable. Regression lines for size and shape models show how the demography and size relationship changes at different quantiles of the given shape variable, with quantile values denoted on the legend for each shape variable. For each response variable, models have an icon indicating the model with the best model metric. (star) the model with the lowest BIC, used as the primary criterion for model selection for inference to ensure robustness against choosing more complex size and shape models over the size-only model. (cross) the model with the lowest AICc, used as a secondary assessment criterion to compare to BIC. (pentagon) the model with the highest psuedo R^2. Numerical model assessment metrics and further details in Table S3.

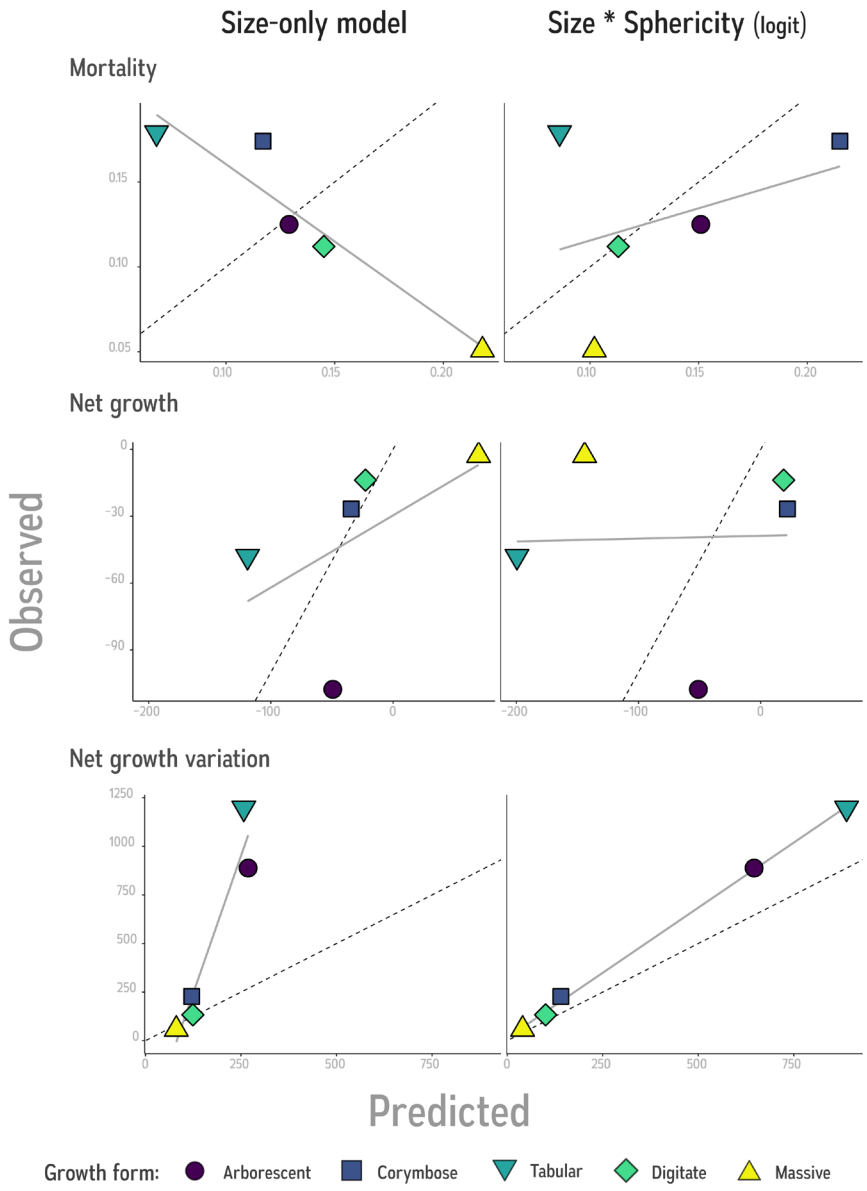


Figure 3. Leave-one-growth-form out analysis for mortality, net growth, and growth variation in reef-building corals, comparing a size-only approach with the size and sphericity model selected previously (fig 2). In each case, data for one growth form was left out of the model fitting process, and the model was used to predict demographic parameters for the left-out growth form, repeated for all growth forms. Observed and predicted values were then compared. Left panels show size only models, right panels show the size interacting with sphericity model. Top row: predicted vs observed mortality probability. Observed mortality probability calculated as the sum of mortality (represented as 1) divided by total colony number for that growth form. Predicted mortality calculated as the mean predicted probability across all colonies for that growth form. Middle row: predicted vs observed net growth. Observed net growth calculated as the mean observed net growth for all colonies in a growth form. Predicted net growth calculated as the mean predicted net growth for all colonies in a growth form. Bottom row: predicted vs observed net growth variability. Observed net growth variability calculated as the standard deviation of net growth across all colonies in a growth form. Predicted net growth variability calculated as the mean of the predicted standard deviation values across all colonies in a growth form. Dashed lines show the 1:1 line indicating perfect accuracy. Black lines show a linear regression line to compare to the 1:1 line as a visual guide only.

Discussion

Results overview

Sphericity is an informative predictor of mortality and growth variation across a broad range of coral sizes and growth forms, with lower BIC and AICc, and higher pseudo-R^2 in all but one case, although the remaining unexplained variation remains high. We were able to predict morphological traits for *in situ* coral colonies with high confidence based on assessing model accuracy via the laser scanned colonies dataset. We then used these predicted morphological traits to capture variation in growth and mortality. We found that volume compactness--captured via sphericity--modulates size-mortality and size-growth variation relationships. No shape variable model explained mean net growth better than the size-only models. The sphericity models were able to predict variation in net growth and mortality for growth forms left out of the model and improved on size-only model predictions. In particular, the sphericity and size model vastly improved the capacity to predict growth variation compared to a size-only model. These results highlight sphericity as a functional trait for coral growth and survival.

Sphericity and volume compactness are functional traits in corals

The underlying cause-and-effect mechanism for how variation in volume compactness explains variation in mortality and growth is not explicitly tested in this study. However, there are strong theoretical arguments for why scleractinian corals have evolved to have a broad range in volume compactness.

Sphericity collapses previously shown growth form-specific variation in growth along a continuous axis of variation. Previous research on the same demography data here shown that mean net growth relationships remained similar across morphological groups whilst varying in the upper and lower quantiles of interannual growth (Dornelas et al., 2017). Here we also see similar patterns where net growth seems to not vary with morphology, yet sphericity captures changes in interannual growth variation. This relationship is further supported by sphericity's predictive power as demonstrated by the leave-one-growth-form out analysis for net growth variation. Whilst these growth forms vary along three axes of volume compactness, surface complexity, and top-heaviness (Zawada et al., 2019a), volume compactness as measured as sphericity appears as a strong candidate for generalising multiple growth-form specific size-growth relationships.

Sphericity also greatly improved on size-only models for explaining variation in mortality. When sphericity is low, and colonies are more morphologically complex, the susceptibility to sources of whole colony mortality such as dislodgement, bleaching, and predation, is much higher compared to sturdier colony shapes. Dislodgment for colonies with high sphericity is more difficult due to more of the colony being attached to the reef matrix and cantilever-effects being reduced for a given force. Bleaching susceptibility of branching colonies has been observed to be higher, possibly due to increased light scattering efficiency in more complex colony shapes acting as a double-edged sword when temperatures are high

(Enríquez et al., 2017). Finally, predation rates on low-sphericity colony shapes can be lower compared to fast growing branching colonies (De'ath and Moran, 1998). Of these explanations for the sphericity-mortality association, the biomechanical links to colony dislodgement are better supported, as are the links to partial mortality which may cause mortality through secondary causes such as disease and tissue damage. Regardless, the predictive power of the leave-one-growth-form out models suggests a strong general link between sphericity and total colony and partial mortality.

Sphericity can supplant surface area to volume ratios as a morphological trait

Sphericity was consistently selected as the most likely shape variable to complement planar area for the demography models. Even with net growth, where the size-only model was selected via BIC, the size and sphericity model has the lowest AICc and the highest pseudo R^2. The selection of sphericity over convexity is less interesting as both are highly correlated and capture similar information and may be a function of differences in predictive accuracy given that the demography models used predicted rather than directly measured morphological variables. However, the comparison to surface area to volume ratio (SA:Vol) is more interesting. SA:Vol ratios are widely used in the literature both historically and in modern research (Hoegh-Guldberg, 1988; Lavy et al., 2015; Reichert et al., 2016). However, the inherent size-conflation of SA:Vol can reduce explanatory power in models as seen in this study. Yet, both sphericity and convexity solve this problem by being size-independent. This allows sphericity to explicitly capture shape-only information, theoretically unconstrained or uncorrelated from colony size. In reality however, sphericity and size are correlated within some growth forms, and this study makes use of those correlations to predict sphericity for *in situ* colonies. Nonetheless, the consistent selection of models including both size and sphericity as predictors suggests that there are tangible affordances of switching from SA:Vol to sphericity as an explanatory functional trait. Doing so also has *zero cost* as sphericity itself is directly calculated from surface area and volume: If you already have measurements or estimates of surface area and volume, you can already calculate sphericity without any additional analysis. Generally, this conclusion applies to any field or study that uses SA:Vol ratios as explanatory variables where partitioning the effects of shape and size are important.

Limitations and future work

There are several caveats associated with this study that should be considered to ground our conclusions. One caveat is that, although each growth form was represented by two to three species, 11 species out of potentially hundreds of different species in the same area is a small sample. Clearly, further work to sample both morphology and demography across a broader range of taxonomic variation would be useful to ensure that the trait-demography relationships outlined in this study hold in multiple contexts.

Further, it should be stated that any trait-demography relationships, whilst underpinned by biological and phenotypic mechanisms, will undoubtedly change with environmental context. Growth form dominance changing with depth and light is well documented (Jackson, 1979) and phenotypic morphological plasticity within the same species or colony underscores this (Brambilla et al., 2022; Hoogenboom et al., 2008). All functional traits—morphology included—interact with the environment to produce an effect (growth) or resist change (mortality). It then follows that any shape-size-growth relationships observed in a high-light high-wave action context will be unlikely to remain unchanged in a low-light low-wave action context. Whilst the effect of environment on the results presented here are controlled for by being constrained to a single reef area their interpretation is also constrained to this context. A clear expansion of the work presented here would be to replicate across environmental gradients, potentially bringing in environmental co-variates directly into the modelling process.

A key challenge for shifting to continuous morphological traits is the time cost of obtaining three-dimensional datasets to calculate them. This is doubly true for *in situ* measurements of colony shape that can be just as costly as some demographic measures. However, previous research has shown strong scaling between colony size and shape within growth forms (Fundakowski et al., 2026; Zawada et al., 2019a) in addition to two-dimensional planar area and shape (House et al., 2018). These relationships can therefore be used to reconstruct three-dimensional traits from field observations of colony size and growth form without needing to measure them directly. Whilst this undoubtedly underestimates the true variation in shape at the assemblage scale, this approach has already shown merit for tracking how the shape of assemblages shifts in response to disturbances (Zawada et al., 2019b) and their subsequent impacts on habitat provision for fish (Fontoura et al., 2020). Whilst predicted traits work well in this study, an obvious next step would be to measure morphological traits directly for the same colonies that are tracked for the demography dataset. This would provide a much more robust causal-link between shape and demography. Further, it would allow growth and mortality to be measured in a more nuanced way. For example, measuring growth as changes in volume or surface area rather than planar area, or capturing partial mortality within a colony. Such studies would be resource intensive but would provide a detailed account of the interplay between colony shape and size, and growth and survival.

Conclusion

Together, the results of this study make a clear case for sphericity as a morphological trait that not only captures a key gradient in coral morphology, but also variation in vital rates. Sphericity also has the capacity to supersede surface area to volume ratios for zero cost to the researcher. Its ability to be predicted for *in situ* colonies using growth form and planar area makes it a suitable indicator for management and monitoring programmes to infer the functional state of an assemblage for low cost with a lower barrier to entry compared to methods assessing species, generating three-dimensional datasets, or measuring

demography directly. This work builds on previous research examining how volume compactness relates to both habitat provision (Fontoura et al., 2020) and responses to disturbances (Zawada et al., 2019b). Given the proliferation of *in situ* 3D coral measurements in recent years and the historical establishment of morphology as a key determinant of coral life history strategies, the time is ripe for researchers to incorporate and further examine the case for volume compactness—measured as sphericity--as a candidate unifying trait for corals.

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Data and code accessibility

Both data and code will be made available once this paper is accepted for publication after peer review.

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Supplementary material

Table S1 – Selected models for predicting morphological traits from growth form and planar area based on highest mean absolute error.

Morphological trait	Growth form	Mean estimate formula	Model coefficients with standard errors	Adjusted R-squared	Mean absolute percentage error	Mean absolute error
Surface area to volume ratio	Massive	log10(SAVol) ~ log10(PlanarArea)	mean (Intercept) coef: -0.184 (+/- 0.056) mean log10(PlanarArea) coef: -0.503 (+/- 0.029) sd (Intercept) coef: -2.912 (+/- 0.151)	0.932	11.295	0.01
Surface area to volume ratio	Digitate	log10(SAVol) ~ log10(PlanarArea)	mean (Intercept) coef: -0.409 (+/- 0.099) mean log10(PlanarArea) coef: -0.176 (+/- 0.046) sd (Intercept) coef: -2.384 (+/- 0.129)	0.328	19.117	0.031
Surface area to volume ratio	Corymbose	log10(SAVol) ~ PlanarArea	mean (Intercept) coef: -0.421 (+/- 0.036) mean PlanarArea coef: -0.001 (+/- 0) sd (Intercept) coef: -2.058 (+/- 0.11)	0.254	27.401	0.078
Surface area to volume ratio	Tabular	SAVol ~ 1	mean (Intercept) coef: 0.277 (+/- 0.02) sd (Intercept) coef: -2.514 (+/- 0.177)	0	29.022	0.073
Surface area to volume ratio	Arborescent	log10(SAVol) ~ 1	mean (Intercept) coef: -0.699 (+/- 0.021) sd (Intercept) coef: -2.501 (+/- 0.177)	0	15.597	0.029
Sphericity	Massive	logit(Sphericity) ~ 1	mean (Intercept) coef: 1.228 (+/- 0.086) sd (Intercept) coef: -0.907 (+/- 0.151)	0	8.206	0.06
Sphericity	Digitate	logit(Sphericity) ~ log10(PlanarArea)	mean (Intercept) coef: 1.01 (+/- 0.263) mean log10(PlanarArea) coef: -0.759 (+/- 0.121) sd (Intercept) coef: -1.411 (+/- 0.129)	0.566	13.664	0.048
Sphericity	Corymbose	logit(Sphericity) ~ log10(PlanarArea)	mean (Intercept) coef: 0.25 (+/- 0.286) mean log10(PlanarArea) coef: -0.65 (+/- 0.136) sd (Intercept) coef: -1.33 (+/- 0.11)	0.358	16.914	0.043
Sphericity	Tabular	logit(Sphericity) ~ log10(PlanarArea)	mean (Intercept) coef: 0.58 (+/- 0.374) mean log10(PlanarArea) coef: -0.721 (+/- 0.167) sd (Intercept) coef: -1.281 (+/- 0.177)	0.539	18.709	0.05
Sphericity	Arborescent	logit(Sphericity) ~ log10(PlanarArea)	mean (Intercept) coef: 0.846 (+/- 0.399) mean log10(PlanarArea) coef: -0.789 (+/- 0.145) sd (Intercept) coef: 3.469 (+/- 1.933) sd log10(PlanarArea) coef: -2.183 (+/- 0.749)	0.787	8.245	0.022
Convexity	Massive	logit(Convexity) ~ log10(PlanarArea)	mean (Intercept) coef: 1.587 (+/- 0.52) mean log10(PlanarArea) coef: 0.428 (+/- 0.268) sd (Intercept) coef: -0.693 (+/- 0.151)	0.104	3.686	0.033

Convexity	Digitate	logit(Convexity) ~ log10(PlanarArea)	mean (Intercept) coef: 1.021 (+/- 0.427) mean log10(PlanarArea) coef: -0.5 (+/- 0.197) sd (Intercept) coef: -0.927 (+/- 0.129)	0.177	18.826	0.087
Convexity	Corymbose	logit(Convexity) ~ 1	mean (Intercept) coef: -0.868 (+/- 0.068) sd (Intercept) coef: -0.837 (+/- 0.11)	0	25.465	0.074
Convexity	Tabular	logit(Convexity) ~ log10(PlanarArea)	mean (Intercept) coef: 0.701 (+/- 0.468) mean log10(PlanarArea) coef: -0.646 (+/- 0.209) sd (Intercept) coef: -1.056 (+/- 0.177)	0.375	21.89	0.074
Convexity	Arborescent	logit(Convexity) ~ log10(PlanarArea)	mean (Intercept) coef: -0.313 (+/- 0.701) mean log10(PlanarArea) coef: -0.516 (+/- 0.272) sd (Intercept) coef: -1.36 (+/- 0.177)	0.184	18.109	0.031