**Calcification, respiration, and photosynthesis rates of six prominent coral taxa**

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**Abstract**

Coral reefs provide a range of important services to humanity, which are underpinned by community-wide ecological processes such as coral calcification and fish growth. Estimating these processes relies on our knowledge of organismal physiology and species-specific abundances in the field. For colonial animals such as reef-building corals, abundance is frequently expressed as the percentage of live coral cover, a metric that does not account for demographic parameters such as coral size. This is problematic because many physiological processes exhibit non-linear scaling over ontogeny, and failure to account for these patterns may skew estimates of ecosystem functioning. In the present study, we characterise the ontogenetic scaling of three physiological rates — calcification, respiration, and photosynthesis — for six prominent, reef-building coral taxa in Mo’orea (French Polynesia). Our results indicate that across all taxa, area-specific calcification rates are higher for smaller colonies. However, photosynthesis and respiration rates remain constant over the colony-size gradient. Furthermore, we identify considerable species-specific variation by revealing correlations between the ratio of net primary production and calcification and recent demographic dynamics of these six coral species. Therefore, intraspecific scaling of reef-building coral physiology not only alters our understanding of community-wide coral reef functioning, but it also explains species’ responses to disturbances.

**Introduction**

Coral reefs are among the most diverse marine ecosystems and provide essential services to more than 500 million people worldwide (Hoegh-Guldberg 2011). Healthy coral reefs protect coastlines from wave energy, reduce the risk of coastal flooding (Harris et al. 2018), and provide local populations with crucial food supplies (Cinner et al. 2020). While there is broad agreement on which processes are fundamental for reef systems, our capacity to quantitatively define a ‘functional’ reef is still limited (Kennedy et al. 2013, Hughes et al. 2017, Brandl et al. 2019a). For example, fish-based herbivory can help corals to settle and grow. However, the cumulative rate of herbivory, as well as the species identities critical for facilitating this process, remain poorly resolved and may vary greatly among reefs (Mumby 2009, Arnold et al. 2010). Similarly, coral calcification is key to reef accretion, but the rates of calcification needed to keep up with sea level rise and their dominant drivers remain largely unquantified (Perry et al. 2018).

One reason why defining ‘functional’ reefs remains challenging is that functional studies on coral reefs traditionally employ qualitative, categorical traits as a proxy for functioning, but our capacity to directly quantify processes is still limited (Brandl et al. 2019a). Integrating empirically-measured processes into quantifications of reef functioning has been performed using two main approaches: i) the direct measurement of *in situ* elemental fluxes and ii) the scaling of individual-level physiological processes to the community level using an additive approach (Allen et al. 2005, Barneche et al. 2014). Direct measurements of elemental fluxes is the most accurate method to quantify ecological functioning (Nakamura & Nakamori 2009). However, direct assessments are labour intensive and subject to local, current conditions, and they are thus impractical for integrating research across large spatial and temporal scales. In contrast, the scaling up of organismal physiological processes to community-wide fluxes has been used to successfully estimate large-scale biomass production and nutrient cycling in coral reef fishes (Allgeier et al. 2014, Brandl et al. 2019b, Morais et al. 2020, Schiettekatte et al. 2020), as well as calcification and accretion in coral assemblages (Perry et al. 2012). While this method can leverage widely-available datasets of fish or coral community structure, reliable estimates inevitably depend on the availability and accuracy of physiological measurements conducted at both species and individual levels (Edmunds & Riegl 2020).

At the physiological level, corals consume dioxygen (O2)through respiration and produce O2 due to their symbiotic association with photosynthetic microalgae from the Symbiodiniaceae family (LaJeunesse et al. 2018). The coral host provides their symbiotic algae with a protected environment and essential compounds such as respiratory carbon dioxide (CO2) and nitrogenous waste, which are necessary for the symbiotic algae to photosynthesize (Muscatine & Porter 1977, Barnes 1987, Birkeland 1997). In turn, the coral host receives photosynthetically fixed carbon that may support up to 95% of its metabolism (Muscatine 1990), including skeletal growth through biocalcification (i.e., calcification rate) (Barnes 1987, Muscatine 1990, Birkeland 1997, Barnes & Hughes 1999). These basic physiological processes are essential to ecological functioning at community level since calcification, respiration, and photosynthesis are interconnected elemental fluxes that allow the reef system to persist and accrete (Howard et al. 2017). Therefore, accurate quantifications of species-specific rates of calcification, respiration, and photosynthesis rate are necessary to extrapolate system-wide functioning based on coral community structure (Madin et al. 2016).

Several studies on coral calcification have highlighted that coral growth may be allometric (i.e., exhibiting varying rates according to colony size) (Edmunds & Burgess 2016, Dornelas et al. 2017) instead of isometric (i.e., exhibiting constant rates across colony size). Specifically, the growth rate of large colonies is substantially lower than that of smaller coral colonies, but the mechanisms behind this pattern remain unclear. For example, larger colonies may invest substantial energy in reproduction, which reduces the energy available for growth (Richmond 1987). Likewise, larger colonies can experience higher partial mortality (e.g., localized tissue necrosis, overgrowth by other organisms, and predation from parrotfishes), which may also reduce growth rates (Pratchett et al. 2015, Madin et al. 2020). Understanding whether and why organismal growth rates are isometric or allometric has important implications for our capacity to estimate community-level fluxes. Indeed, most community data report the substrate covered by each species without recording the size of individual colonies (Flower et al. 2017, Edmunds & Riegl 2020). Therefore, the estimation of community functions using the additive framework will be accurate only in the case of isometry. On the other hand, in the case of allometry, we need information on colony size distribution to properly calculate community-level fluxes.

In the present study, we quantify three primary physiological functions (*i.e.,* calcification, respiration, and photosynthesis) for six coral taxa along a gradient of colony size to examine whether each species exhibits an isometric or allometric pattern. Furthermore, we investigated whether a coral genus may have an energetic advantage (i.e., through those three primary physiological functions) as a potential mechanism to explain its distribution compared to other species.

**Material and Methods**

Coral species selection, preparation, and acclimation

In September 2018, we collected 384 coral colonies from six coral taxa: *Acropora hyacinthus, Astrea curta, Montipora verrilli, Napopora irregularis, Pocillopora* cf. *verrucosa* and massive *Porites sp.* These taxa exhibit unique life-history strategies and are among the most abundant reef-building coral species in Mo’orea (Putnam et al. 2012, Darling et al. 2019). Although we were able to identify five taxa to the level of species in the field, we were unable to distinguish massive *Porites* beyond the genus level because *P. lutea* and *P. lobata* are macro-morphologically indistinguishable. We sampled all coral colonies at a depth of 11–13 m on the outer reef of the northern coast of Mo’orea. Before each collection, we recorded the following environmental parameters *in situ*: mean ambient seawater temperature, salinity, and photosynthetically active radiation (PAR: 400-700 nm). We collected colonies from the substratum using a hammer and chisel and transported them to the lab in a cooler filled with seawater. Transportation took approximately 15 minutes.

In the laboratory, each colony was quickly cleaned with Milli-Q water and epibionts or epiphytes were carefully removed. We attributed each colony to a size class: (S1) <100 cm2, (S2) 100-400 cm2 and (S3) >400 cm2 for further physiological measurements. Finally, we placed all colonies into tanks conditioned to reflect *in situ* environmental parameters and gave the colonies 7 days to recover and acclimate.

Respiration and photosynthesis

We assessed coral physiology using intermittent-flow respirometry, where colonies were immersed in chambers connected to both a closed recirculating pump system and an open flush-pump system to periodically record oxygen concentrations in the water. The colonies were incubated in permeable chambers of three different volumes ranging from 0.5 L to 1 L to 4 L, which were selected according to the ratio between incubation volume and colony size. Colonies smaller than 100 cm2 were incubated in 0.5 L chambers, colonies between 100 and 400 cm2 were incubated in 1 L chambers, and colonies larger than 400 cm2 were incubated in 4 L chambers. For each respirometry trial, we assessed four controls and four corals of each size class (n = 12 colonies for each trial). Since we measured both photosynthesis and respiration, we measured of O2 concentrations in the chambers both in light and dark conditions. For each trial, we exposed colonies to light for three hours, then we turned off the light and started recording O2 consumption 30 minutes later. We limited the dark phase to 1 hour to prevent O2 concentrations from falling below 80% saturation (Kolb 2018). O2 concentration was recorded with PyroScience FireSting optical oxygen meters (Pyroscience GmBH, Aachen, Germany). We removed the first thirty minutes of each trial, which corresponded to the stabilization of the O2 concentration slopes in the closed stage of the system. For each trial, we included a chamber that was not populated with a coral colony to account for background bacterial respiration. Using these blanks, we corrected O2 concentrations for each trial, ultimately yielding two consumption profiles: one that corresponded to physiological activity in daylight (i.e., non-distinction of the respiration and photosynthesis activities and corresponding to the net photosynthesis) and the other in nocturnal conditions (i.e., respiration). All oxygen concentrations are described in mg (O2) h-1. The respirometry system was bleached after each trial to minimize background respiration by the accumulation of microorganisms.

Calcification

We collected 50 mL of water from each incubation chamber and the control chambers, both in light and dark conditions. We stored the samples in sealed, opaque vials in the dark at 4°C, then we allowed them to stabilize for 2 hours at room temperature (25°C) before processing. We carried out three titrations per sample to define total alkalinity using a Titrando 888 (Metrohm) and Titripur c(HCl) (with a concentration of 100 mmol L-1). We defined titration controls with water samples collected before coral incubations. We calculated calcification rate based on the difference between total alkalinity measured at the beginning and end of each incubation period (∆AT) (Dickson et al. 2007). Specifically, we assumed that one mole of CaCO3 is produced when alkalinity (∆AT) drops by two moles across a fixed time period (∆t) (i.e., - ∆AT/2∆t), then by multiplying these parameters by seawater density (ρsw). Finally, we converted the resulting value to g cm-2 yr-1 based on the molar mass of CaCO3.

Colony-size estimation using photogrammetry and out-planting

After each incubation, we took 100 to 200 overlapping high-resolution photos (300 dpi) of each colony. The photos were used to construct 3D models using the Agisoft PhotoScan software (LLC 2016), which allowed us to define the volume and live surface area of each colony (Harwin et al. 2015). All coral colonies (i.e., n = 384) were then placed in a large aquarium and ultimately returned to their natural habitat on the outer reef.

Statistical analysis

Before analysing the data, we removed data points if 1) a coral colony exhibited a negative calcification rate (i.e., dissolution), 2) the tank temperature dropped below 27°C (i.e., failure of the tank heating system), or 3) the linear fit of O2 concentrations over time to quantify respiration or net photosynthesis rates exhibited an R2 value lower than 0.8 (Kolb 2018). Following this quality control procedure, we retained 250 out of 384 (65 %) of data points for the analysis. We then applied Bayesian models to estimate the relationship between colony size and each physiological rate on the natural log scale using the R package *brms* (Bürkner 2017). Our models were specified with the following structure:

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where is the natural logarithm of the rate of calcification (kg yr-1), O2 consumption (mg h-1),or O2 production (mg h-1) of species and individual ; is the natural logarithm of live coral surface area (cm2); is the among-species average intercept on the natural log scale; is the among-species average size scaling slope (i.e., exponent on the natural scale); is a vector comprising levels of species (*n* = 6), which, in turn, create a hierarchical matrix of rows and two columns, respectively, representing species-level additive deviations from and ; is the Cholesky factor of the correlation matrix between the hierarchical effects, is the two-by-two diagonal matrix whose diagonal is a vector of among-species standard deviations (), and is an -by-two matrix of standardised hierarchical effects. The prior sampling distributions were specified to follow Gaussian ((location, scale)), Gamma ((shape, inverse scale)) and log-LKJ (LKJ(shape)). We ran our models with three chains, 5,000 draws per chain, and a warm-up period of 2,500 steps, thus retaining 7,500 draws to construct posterior distributions. We verified chain convergence with trace plots and confirmed that Rhat (the potential scale-reduction factor) was lower than 1.05 (Gelman et al. 1992). We obtained R2 values of 0.92, 0.77, and 0.77 for the calcification rate model, respiratory rate model, and photosynthetic rate model, respectively (Table 1, Fig. S1). We then divided our raw data by the respective surface area of each colony to express rates on an area-specific basis. To calculate the posterior distribution of the scaling exponent of area-specific rates against colony area, we used 1- (Fig. S2).

The ratio between net photosynthesis rate and calcification has been used as a proxy for how much energy is available to perform other functions (e.g., reproduction) (Rinkevich 1989). To do so, we performed simulations to evaluate the energy budget of monospecific assemblages. Specifically, we first defined average colony size for the six genera according to three simplified scenarios (Kayal et al. 2018): 1) dominance of small colonies, 2) even size distribution, and 3) dominance of large colonies. Because on reefs around Mo’orea, a series of recent disturbances have shifted coral composition in favour of Pocillopora corals (Adjeroud et al. 2018), we chose to confront *Pocillopora vs.* the other genera. For each scenario, we randomly generated 100 size distributions which were used to calculate species- and size-specific photosynthesis and calcification rates. These estimates were used to compare population-wide estimates of *Pocillopora sp*. against each of the other five species (i.e., *Acropora hyacinthus, Astrea curta, Montipora verrilli, Napopora irregularis* and *Porites spp*.). Finally, we estimated the ‘energetic ratio’ for each population. All the statistical analyses were run in R version 4.0.3 (R Core Team 2019).

**Results**

For all coral species, we observed a linear increase in calcification, respiration, and photosynthesis across the colony-size gradient on the log-log scale (Fig. 1). However, we identified both hypo-allometric and isometric relationships, depending on the physiological process. Calcification showed a hypo-allometric relationship with colony size, as evidenced by values of that were lower than 1 (Table 1., Fig. 1). Although massive *Porites* spp., massive *Astrea curta*, and encrusting *Montipora verrilli* had higher values than the other species, only 2% of the 5,000 posterior draws had a slope greater than 1. On the other hand, respiration and photosynthesis increased isometrically with colony size, as demonstrated by that did not differ from 1.

Whole colony calcification rates were hypo-allometric; thus, calcification rates per unit surface area decreased as colony size increased for all species, while photosynthesis and respiration per unit area were not size dependent for all species. However, we detected substantial among-species variation in the coefficients (i.e., the species-specific intercepts) for all three physiological processes (Fig. 1, Table 1). Indeed, *Acropora hyacinthus* showed the highest calcification, while *Montipora verrilli* exhibited the lowest calcification. Yet, this trend was reversed for both respiration and photosynthesis, where *Montipora verrilli* showed and *Acropora hyacinthus* showed the highest and lowest rates, respectively. Further exploring the species-specific relationships between photosynthetic rates and calcification rates, we detected two main trends (Fig. 2). First, *Porites* spp., *Napopora irregularis*, and *Acropora hyacinthus* showed higher calcification rates than net photosynthetic rates, while *Astrea curta, Montipora verrilli,* and *Pocillopora* cf. *verrucosa* showed the opposite pattern. Using these ratios to model population-wide processes under hypothetical size structure scenarios, we found that monospecific stands of *Pocillopora* cf. *verrucosa* exhibited the highest rates of calcification vs. photosynthesis, regardless of population structure (i.e., ratio ~ 3.5; Fig. 2).

**Discussion**

Organismal physiology underpins community-wide ecological processes that define ecosystem functioning. On coral reefs, coral calcification is the process responsible for habitat creation, reef accretion, and coastal protection. We analysed three fundamental physiological functions (i.e., calcification, respiration, and photosynthesis) for six prominent coral taxa to test whether the relationships of these functions with colony size was isometric or allometric. Similar to recent results (Edmunds & Burgess 2016, Dornelas et al. 2017, Madin et al. 2020), we found that calcification per unit area increases hypo-allometrically across all six species. However, this was not the case for photosynthesis and respiration, which scaled isometrically with colony size. Previous work has highlighted allometry in respiration and photosynthesis in *Pocillopora sp.* (Edmunds & Burgess 2016). The prevalence of an isometric relationship across the six species in our study suggests that isometric scaling of respiration and photosynthesis rates may be common across coral ontogeny, at least at comparable climatic conditions.

The isometric scaling of photosynthesis, as opposed to the allometric scaling of calcification, emphasizes the potential importance of coral growth in early life stages. Small, recently settled colonies generally experience intense mortality (Ritson-Williams et al. 2009, Penin et al. 2010, Wall & Stallings 2018), and a rapid increase in colony size (through extensive calcification) may offer the best chance for survival (Heino & Kaitala 1999, Doropoulos et al. 2012). Thus, while it is beneficial for small coral colonies to disproportionally invest in calcification, there are no immediate benefits from increased photosynthesis. In fact, high photosynthesis per unit surface may hamper early-life stage success through exposure to oxidative stress (Fitt et al. 2001, Hoogenboom & Anthony 2006).

While the examined coral species showed comparable scaling relationships for calcification rates, *A. hyacinthus* had a consistently higher rate than the other species. These results are consistent with the high calcification rates documented for corals in the genus *Acropora*, which are generally classified as fast-growing corals (Huston 1985, Harriott 1999, Anderson et al. 2018). However, although *A. hyacinthus* had the highest calcification rate, its photosynthetic and respiratory rates were among the lowest in our experiments. This provides physiological evidence that *A. hyacinthus* tends to allocate most of its energy to growth, rather than other essential processes (e.g., increasing skeletal density, reproduction) (Razak et al. 2020). Conversely, *M. verrilli* and *P. verrucosa* had the highest photosynthetic rates (Fig. 1, Fig. S2) but markedly lower calcification rates than *A. hyacinthus*, which further highlights differences in the life-history strategies of the various species. For instance, Ward *et al*. (1995) suggested that high lipid concentrations (which arise from increased photosynthesis) correlate with reproductive activity, suggesting higher resource allocation to reproductive tissues in *M. verrilli* and *P. verrucosa*. For *Pocillopora*, at least, brooding sperm and egg bundles may require this investment and subsequently enhance the chances of *Pocillopora* offspring to survive(Hirose et al. 2001). Indeed, the high photosynthetic rate of *P. verrucosa* explains the success of this species in Mo’orea, a reef system recently dominated by pocilloporids (Hédouin et al. 2020). Although *M. verrilli* employs broadcast spawning, it is the second most abundant coral genus in Mo’orea (Bosserelle et al. 2014), suggesting that higher photosynthesis rates are directly related to ecological success under the current environmental conditions in Mo’orea.

The distinct photosynthetic rates among coral taxa might arise from the different physiological and ecological attributes of associated symbiotic communities (Baird et al. 2009, Putnam et al. 2012, Rouzé et al. 2019) and their transmission. *P. verrucosa* generally shows a stable association with the genus *Cladocopium* (Stat et al. 2008, Baker et al. 2018), which exhibits high photosynthetic efficiency and is transmitted vertically to offspring. *M. verrilli* shows a similar association and transmission dynamics (Stat et al. 2015). In contrast, *A. hyacinthus* exhibits flexible association with different Symbiodiniaceae genera, often obtained through horizontal transfer (Davies et al. 2020).While this results in the dominance of acroporids in a variety of environmental conditions, the present community composition around Mo’orea suggests that the physiological profile of *A. hyacinthus* and its variable symbionts are disadvantageous under current conditions, as the genus has become rare as compared to *P. verrucosa* or *M. verrilli* (Babcock et al. 2003). The other three coral species (i.e., *A. curta, N. irregularis,* andmassive *Porites spp.*) show intermediate physiological performance and likewise intermediate abundances around Mo'orea. Thus, the revealed differences in physiological profiles likely determine the energetic basis for processes unfolding at the population and community levels.

In turn, understanding the nature of these scaling relationships opens opportunities to estimate ecosystem-wide processes critical for coral reef functioning. In the case of photosynthesis and respiration, isometric scaling permits relatively simple extrapolations of colony-level processes to entire communities. Specifically, if species identities and the relative combined surface areas of colonies are known, we may be able to compute reasonably accurate estimates of community-wide respiration and photosynthesis. In this case, standard coral survey methods that record the percent cover of different species (English et al. 1997, Hill et al. 2004) allow the estimate of community-level photosynthetic capacity. In contrast, due to the size-dependency of calcification, an accurate estimation of community-levelcalcificationwould require information on the size distribution of individual colonies, which are seldom recorded in standard monitoring (Edmunds & Riegl 2020). Given that calcification is a crucial function performed by coral assemblages, with direct implications for reef accretion (Perry et al. 2018) and wave-energy attenuation (Harris et al. 2018), the absence of colony size from most major coral reef monitoring programs precludes us from inferring community-level processes with a greater accuracy.

In summary, our results expand our understanding of coral physiology and species-specific traits that can confer ecological advantages under changing environmental conditions. Further, our findings strengthen our capacity to predict community-wide rates of photosynthesis and respiration based on commonly collected coral survey data, while simultaneously questioning the utility of most monitoring data that omit colony size in community-wide estimates of calcification. Across many organisms and ecosystems, the documentation of organismal scaling relationships has greatly advanced the mechanistic understanding of ecological processes. Doing so for scleractinian corals, the foundation species of one of Earth’s most diverse and productive ecosystems, will greatly advance our capacity to understand and predict the status of coral reefs.

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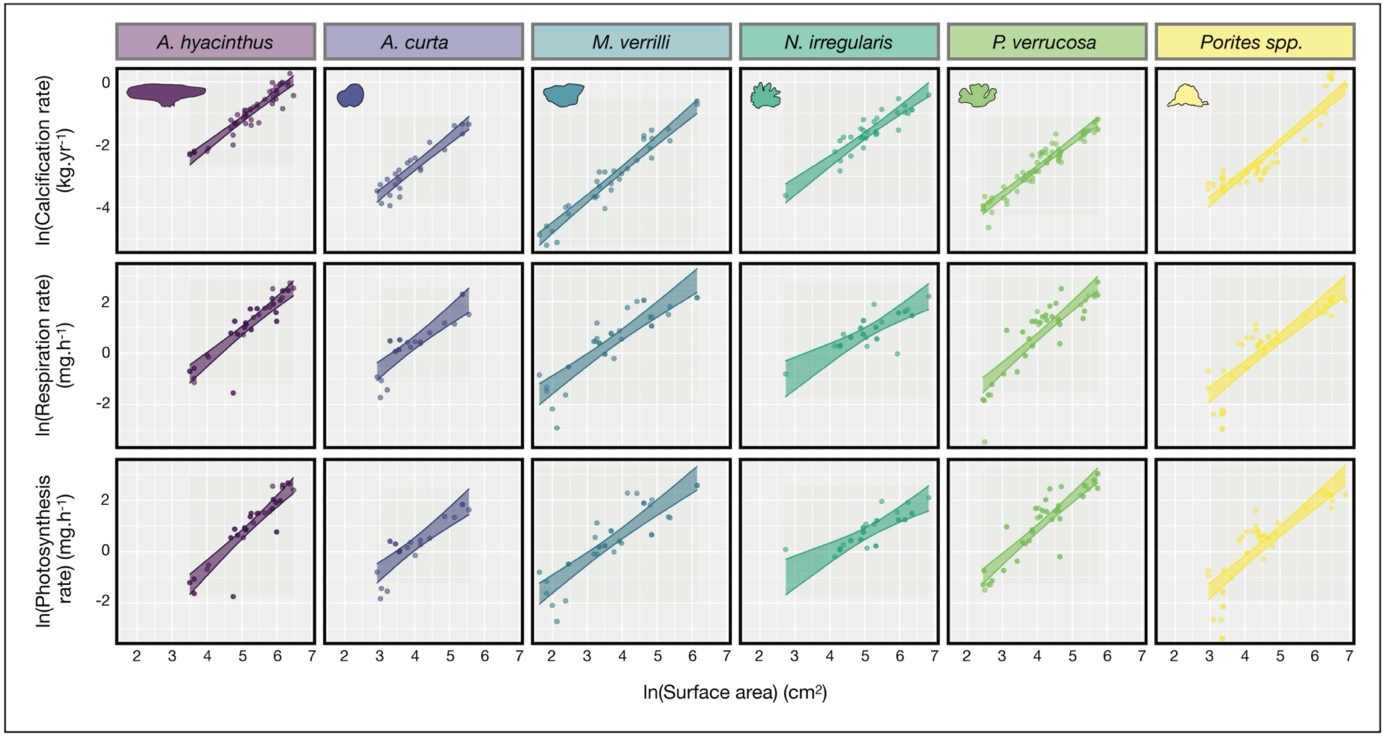


Figure 1 | Scaling relationships between the three physiological processes (i.e., calcification, respiration, and photosynthesis rates, respectively, from top to bottom) and live coral surface area for six coral species (*Acropora hyacinthus, Astrea curta, Montipora verrilli, Napopora irregularis, Pocillopora* cf. *verrucosa* and *Porites* spp.) with a ± 95% Bayesian credible interval. All relationships are depicted on the log-log scale, with dots representing the raw data and regression lines representing posterior predictions from the Bayesian linear model (± 95% credible intervals). Coral silhouettes represent the mature coral morphology.

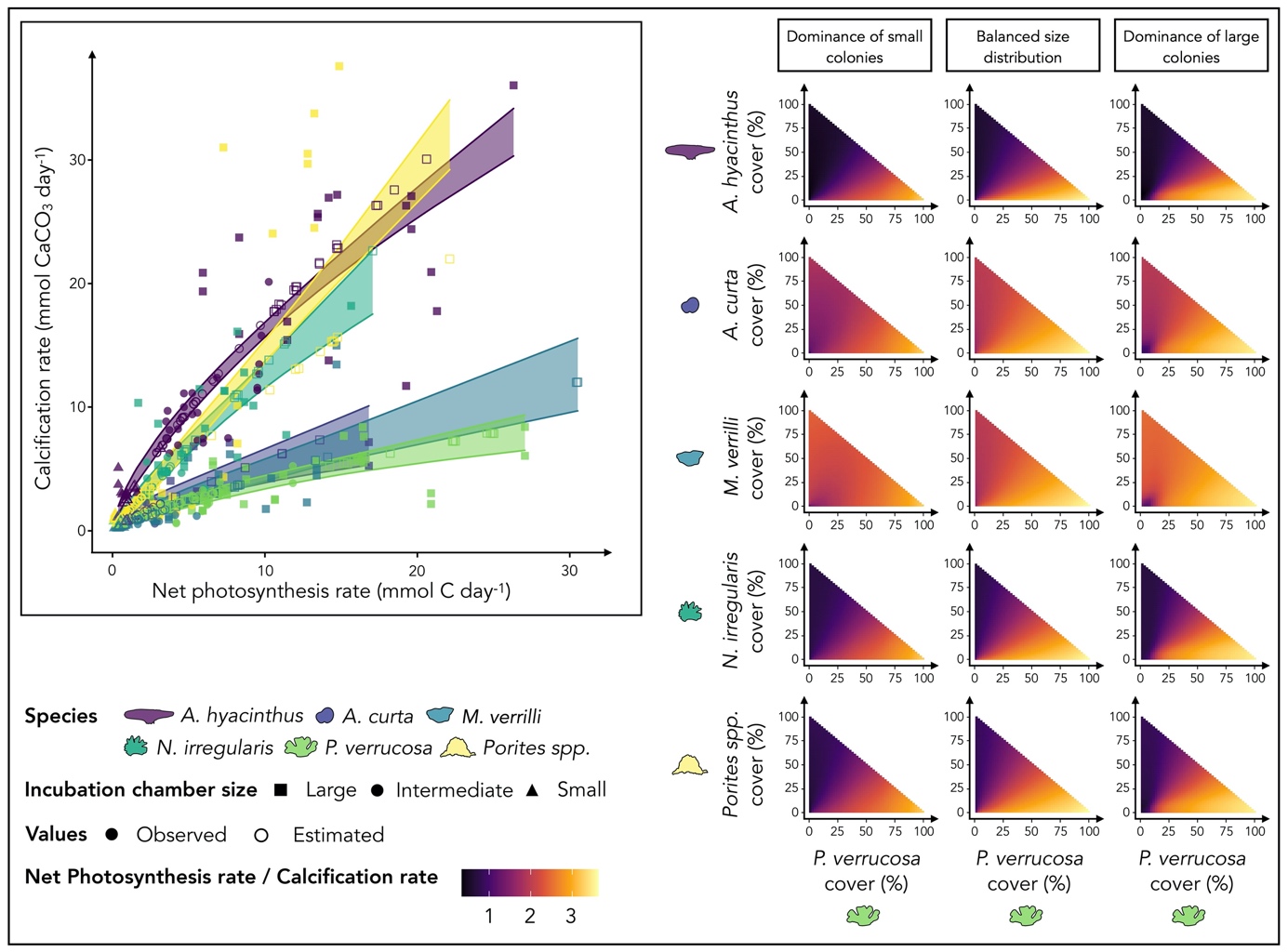


Figure 2 | Representation of hypothetical coral assemblages and their corresponding energy ratios (net photosynthesis rate/calcification rate). The plot on the left shows relationships between calcification and net photosynthesis, which underpin the community-wide models. Estimates from previous Bayesian models (unfilled points) were added to our observations (filled points). Matrices on the right represent scenarios of *Pocillopora* cf. *verrucosa* cover vs other species (*Acropora hyacinthus, Astrea curta, Montipora verrilli, Napopora irregularis,*andmassive *Porites*). The three columns represent three size-structure scenarios.

Table 1 | Point estimates and 95% credible intervals for fitted parameters based on Bayesian linear models estimating calcification, respiration, and photosynthesis rates based on colony size and species identity.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Calcification** | | | **Respiration** | | | **Photosynthesis** | | |
| **Parameters** | **Mean** | **2.5%** | **97.5%** | **Mean** | **2.5%** | **97.5%** | **Mean** | **2.5%** | **97.5%** |
| **Fixed effects** | | | | | | | | | |
| ln(⍺) | -6.126 | -6.719 | -5.486 | -4.154 | -5.565 | -2.741 | -3.971 | -5.074 | -2.907 |
| ß | 0.881 | 0.792 | 0.966 | 1.074 | 0.796 | 1.351 | 1.033 | 0.800 | 1.256 |
| **Random effects** | | | | | | | | | |
| Std. Deviation of ln(⍺) | 0.613 | 0.228 | 1.408 | 1.437 | 0.624 | 3.006 | 1.081 | 0.383 | 2.376 |
| Std. Deviation of ß | 0.075 | 0.006 | 0.199 | 0.281 | 0.100 | 0.638 | 0.221 | 0.050 | 0.519 |
| Correlation of ln(⍺) and ß | -0.58 | -0.98 | 0.527 | -0.602 | -0.959 | 0.236 | -0.507 | -0.953 | 0.536 |

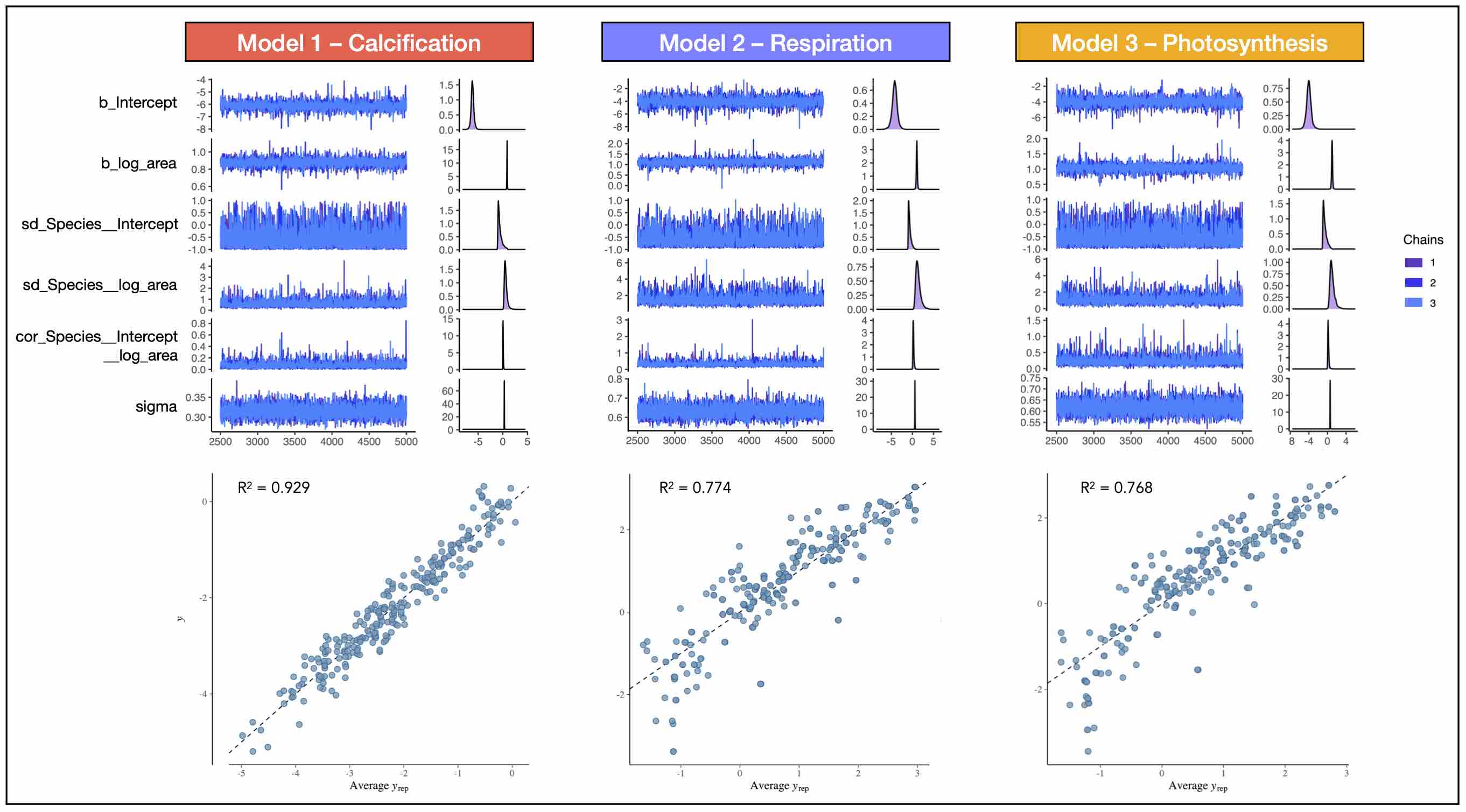


Figure S1 | Trace plots depicting the Monte Carlo chains from the three Bayesian models. Each model (i.e., calcification, respiration, and photosynthesis) was run with three chains of 5,000 iterations, with the first 2,500 steps discarded. The scatterplots represent posterior predictive checks with the respective R2 values estimated from the model.

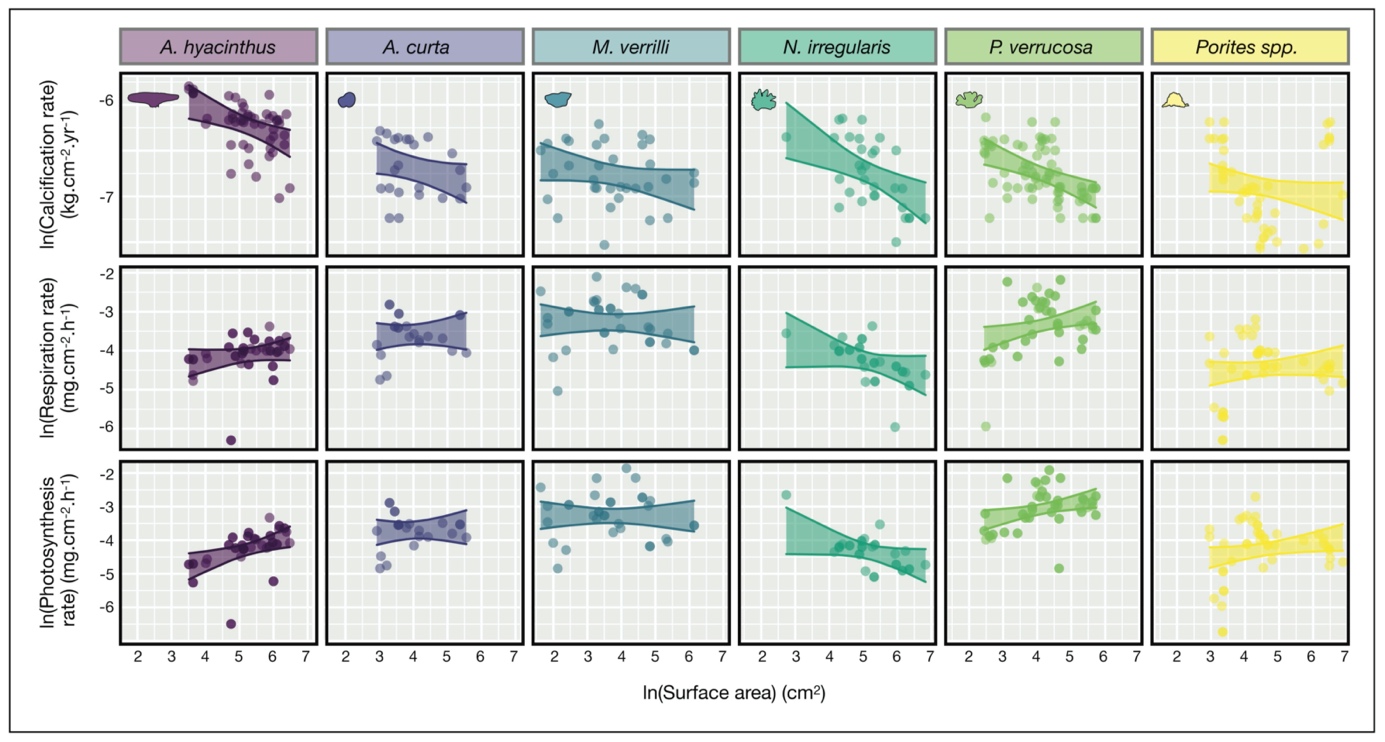


Figure S2 | Relationship between the surface area-specific physiological processes (calcification, respiration, and photosynthesis rates, respectively, from the top to the bottom) and live coral surface area for six coral species (*Acropora hyacinthus, Astrea curta, Montipora verrilli, Napopora irregularis, Pocillopora* cf. *verrucose,* and *Porites spp.*) with a ± 95% Bayesian credible interval. All relationships are depicted on the log-log scale, with dots representing the raw data points and regression lines representing posterior predictions from the Bayesian linear model (± 95% credible intervals). Coral silhouettes represent the current mature coral morphology.