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Research Article

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Posted Date: November 11th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11114238/v1

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Additional Declarations: No competing interests reported.

Using photogrammetry to examine how coral host size and architecture relate to *Gobiodon* body morphology and group size

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Abstract. The size and structural architecture of a microhabitat can influence a wide range of an organism's biological and ecological traits. In the strongly microhabitat-associated, coral-dwelling genus *Gobiodon,* body morphology appears as a unique adaptation to their obligate *Acropora* spp. coral hosts. These fishes often form social groups within a single coral colony, which they can inhabit throughout their adult lives. Using photogrammetric reconstructions of 72 coral colonies, *in situ* coral health estimates, body morphology measurements and counts of resident gobies, we tested whether the size and structure of *Acropora* hosts were associated with variation in body morphologies and social group size in three poorly studied *Gobiodon* species: *G. axillaris, G. citrinus,* and *G. sp.* We found strong alignment between coral host structure and the body morphologies in all three species. The larger, more openly branched corals occupied by *G. citrinus* aligned with its larger and broader body form. In contrast, the smaller-bodied congeners occupied smaller, more rugose and densely branched colonies, with *G. axillaris* exhibiting significantly greater elongation and lateral compression while occupying densely packed corals. We also found that group size increased with coral surface area in all three species. We found no relationship between coral health and fish group size in any of the focal species. These findings highlight the close relationships between obligate coral-dwelling fishes and their threatened host habitats, demonstrating species-specific associations between coral structure, fish morphology, and social organisation that appear to be facilitated by the evolution of body size and shape.

Keywords: *Acropora,* coral host, *Gobiodon*, group size, morphology, photogrammetry

Introduction

Habitat availability and architecture are fundamental determinants of species distributions and abundance, and can also shape phenotypic variation (McCoy and Bell 1991; Tews et al. 2004). The size and three-dimensional structure of an organism's habitat influences the space available for fundamental functional processes, including movement, shelter, competition, reproduction, and access to resources, and shapes both ecological interactions and biological traits (Morris 2003; Almany 2004; Bell et al. 2012; Graham and Nash 2013; He et al. 2019). These effects are particularly pronounced in habitat specialists that complete most or all of their life cycle within discrete habitat patches, where the physical dimensions of the habitat impose direct constraints on body size, body shape,

and the number of individuals that coexist (Wiens 1976; Futuyma and Moreno 1988; Munday 2004; Devictor et al. 2010; Nash et al. 2013). Across marine systems, habitat architecture has been repeatedly linked to morphological divergence, with structural characteristics favouring body forms that facilitate movement and access to confined spaces (Munday 2001; Wainwright 2007; Noonan et al. 2012; Wilson et al. 2013; Claverie and Wainwright 2014).

Scleractinian corals provide clear examples of discrete three-dimensional microhabitats in marine systems. Colonies offer high quality shelter to small organisms living in the highly predatory environment of coral reefs, but differ substantially in their size, architecture, and complexity through variations in surface area, branch spacing, branch density, and overall colony geometry (Veron 1986; Veron 2000; Todd 2008; Naumann et al. 2009; Guendulain-Garcia et al. 2024). These colony characteristics determine the quantity and configuration of living space available to resident organisms, influencing refuge availability and quality, predator access, and recruitment success (Almany 2004; Kerry and Bellwood 2012; Noonan et al. 2012; Graham and Nash 2013; Pereira and Munday 2016; González-Rivero et al. 2017). Discrete coral habitats have traditionally been described using simple measurements, such as colony diameter or interbranch spacing. Recent advances in three-dimensional photogrammetry technology now allow colony surface area and aspects of their structure to be precisely quantified, providing a more realistic representation of the environment experienced by coral-associated organisms and allowing enhanced opportunity to more clearly understand the depth of the relationship between organisms and their environment (Reichert et al. 2017; Zawada et al. 2019a; Bongaerts et al. 2021).

Few reef fishes exhibit a closer association with habitat architecture than coral-dwelling gobies from the genus *Gobiodon* (Bleeker 1856). These small-bodied fishes are obligate inhabitants of specific corymbose *Acropora* coral species, within which they feed, shelter, reproduce, and typically spend their entire post-settlement lives (Munday et al. 1997; Munday 2000; Dirnwöber and Herler 2007; Herler et al. 2011). Most species display strong host specificity and limited movement among coral colonies, resulting in distributions that closely track the availability of suitable host corals (Munday 2000; Schiemer et al. 2009). Consequently, individual coral colonies function as discrete habitat patches in which both ecological interactions and social organisation are constrained by the physical characteristics of the host. Larger colonies provide greater refuge space and breeding habitat and can therefore support larger social groups, whereas smaller colonies frequently host fewer or even solitary individuals (Munday et al. 1998a; Hobbs and Munday 2004; Schiemer et al. 2009).

The physical architecture of host corals may also impose important constraints on the body size and shape of the fishes they support. Because *Gobiodon* live almost their entire life cycle within the interbranch spaces of their hosts, the architecture of these corals provides that they occupy and through which they move (Munday 2001; Vytopil and Willis 2001; Untersteggaber et al. 2014; Wehrberger and Herler 2014). Comparative studies have shown that branch spacing and colony architecture influence both habitat selection and body form, with species occupying more compact colonies generally exhibiting greater lateral compression and reduced body size, allowing access to narrower interbranch spaces (Untersteggaber et al. 2014; Wehrberger and Herler 2014). Recent advances in three-dimensional photogrammetry now provide the resolution needed to distinguish habitat size from specific architectural features, offering an opportunity to refine these host-coral relationships and better resolve the extent of morphological specialisation among *Gobiodon* species.

Most ecological research on *Gobiodon* has focused on a small number of model species and locations, leaving the diversity and specificity of host-coral relationships across the genus poorly understood and virtually

unexamined along Western Australia's coastline. This gap persists despite the abundance and widespread distribution of *Gobiodon* and their specialised use of distinct coral hosts. Understanding how host-colony architecture influences fish morphology and social organisation is increasingly important as ocean warming and acidification threaten highly vulnerable *Acropora* (particularly corymbose forms) that many reef fishes are associated with (Pratchett et al. 2008; Schiemer et al. 2009; Muko et al. 2013; Coker et al. 2014; Manullang et al. 2020). The need for such research is particularly acute at Nyinggulu, where habitat-forming *Acropora* have experienced widespread bleaching during the record-breaking 2024—2025 marine heatwave (Quigley 2025), which was exacerbated by further disturbance from Tropical Cyclone Narelle in 2026 (Bureau of Meteorology 2026). Such consecutive disturbance events can compound habitat loss by causing coral mortality, breakage, and erosion of three-dimensional reef structure (Cheal et al. 2002; Fabricius et al. 2008). For obligate coral-dwelling fishes such as *Gobiodon*, this degradation directly threatens the living space, shelter, and reproductive habitat on which they depend.

Here, we quantify the three-dimensional architecture and health of *Acropora* host colonies and examine how their physical characteristics relate to body morphology and social group size in three poorly studied coral gobies: *Gobiodon axillaris, G. citrinus,* and *G. sp.* Using photogrammetric reconstructions of host colonies, we first test whether occupied corals differ in size and architecture among species and test whether interspecific variation in body morphology reflects differences in host architecture. We then examine whether social group size increases with coral health and the amount of living space and structure provided by host colonies. We hypothesise that (1) host coral architecture and body morphology differ among the three *Gobiodon* species, (2) body size, width, and depth correspond to differences in the surface area, rugosity, and branch packing of coral hosts, and (3) larger, more structurally complex, and healthier coral colonies support larger social groups by providing greater habitable space and shelter.

Methods

Study site

This study was conducted on Manimanira (Five Fingers) Reef, Coral Bay, Western Australia (23°10'44.0" S, 113°45'46.0" E; Fig. 1) during the months of May to July 2025 and 2026. Coral Bay is centrally located along the 300 km World Heritage listed Nyinggulu (Ningaloo) Reef system. Despite the 2024-2025 bleaching event and Tropical Cyclone Narelle in March 2026, widespread bleaching and coral mortality were not evident at Manimanira during our surveys, and the abundances of our focal *Gobiodon* species were high. However, some small nearshore colonies observed following the cyclone were smothered by sediment. These colonies were unoccupied by *Gobiodon* and therefore fell outside our sampling design, which was restricted to occupied colonies. Coral health was nevertheless recorded for each focal colony to quantify variation in host condition and examine its relationship with resident group size.

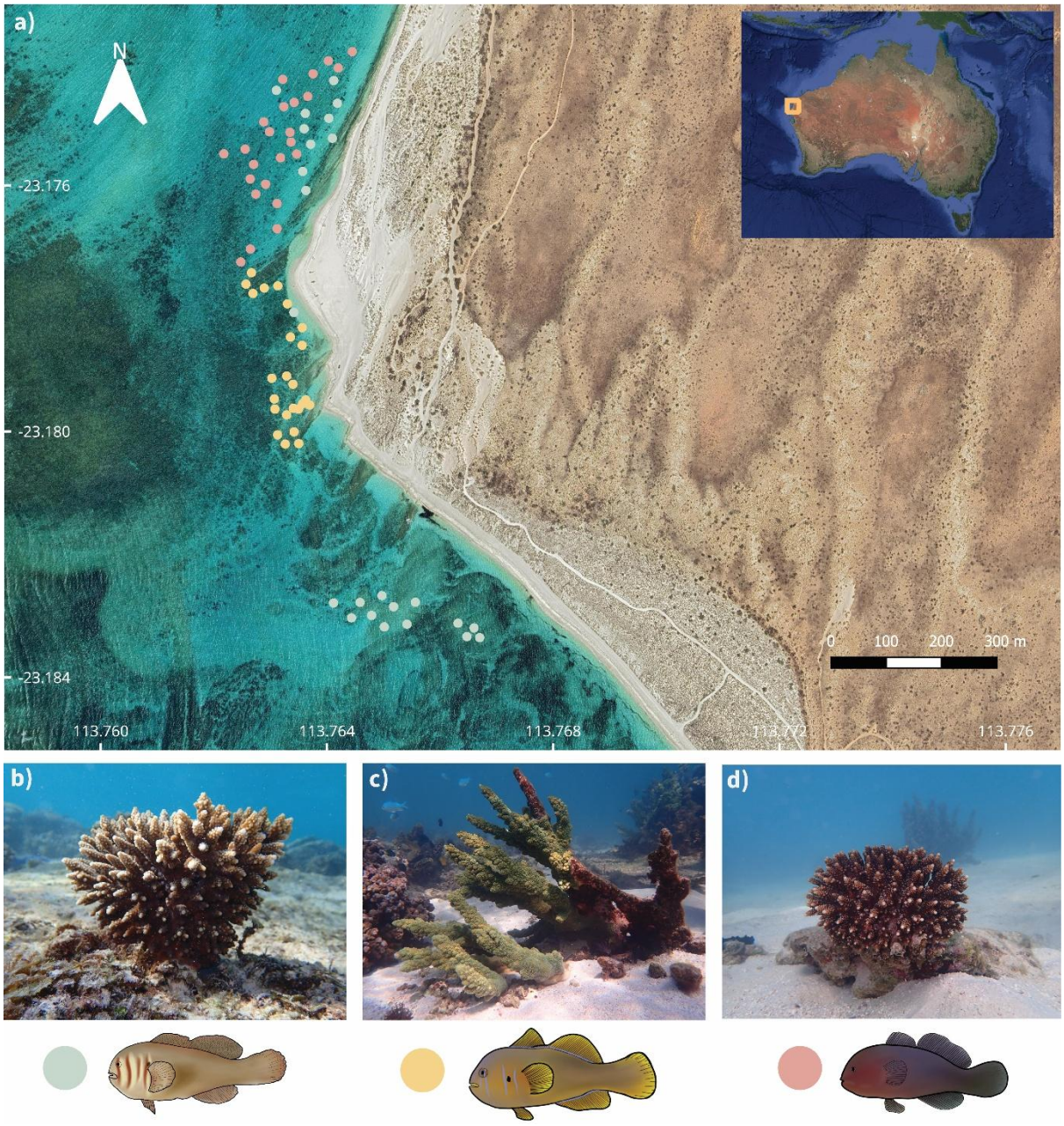


Fig. 1 (a) Map of Manimanira (Five Fingers) Reef in Nyinggulu (Ningaloo) Marine Park, Western Australia (23°10'44.0" S, 113°45'46.0" E). Dots represent the coordinates of *Acropora* spp. coral colonies hosting (b) *Gobiodon axillaris* (green; *Acropora acervata*), (c) *Gobiodon citrinus* (yellow; *A. protoeiformis*), and (d) *Gobiodon sp.* (red; *Acropora sp.*). Illustrations by Sophie Jones.

Coral colony surveys

A total of 72 coral colonies hosting *Gobiodon axillaris*, *G. citrinus*, and *G. sp.* (n = 24 per species) were haphazardly selected across a broad range of sizes and degree of spatial isolation. *G. axillaris* were observed and sampled from *Acropora acervata, G. citrinus* from *A. protoeiformis,* and *G. sp.* from an undescribed yet distinct *Acropora* species from that of *A. acervata,* in that it was redder in colour and formed larger, less circular colonies

(see Fig. 1 or Supplementary Tables 1-3). The coordinates and depth (m) of each colony were recorded, with coral colonies occurring between 1.0 to 3.5 m. Coral health was assessed *in situ* using the CoralWatch Coral Health Chart (Siebeck et al. 2006). The chart was held next to each colony, and the colour of the tissue was visually matched to the closest reference square on the six-point brightness scale. Lower scores indicated paler or bleached (unhealthy) tissue, whereas higher scores indicated darker, more strongly pigmented (healthy) tissue; naturally pale growing tips were excluded when matching colony colour to the chart.

Each colony was photographed using an Olympus TG7 waterproof compact digital camera and following a published protocol (Roach et al. 2021). Eight overlapping image sweeps were completed per colony: two anticlockwise passes around each of the base, middle, and upper sections, and two directly above the colony. Images were captured sequentially at one photograph per 2 s from approximately 50 cm, with a 30-cm ruler positioned on the colony, or on the adjacent benthos for smaller colonies, to scale the resulting three-dimensional reconstruction.

Fish collections and body morphology measurements

Following coral photogrammetry and health surveys, all resident *Gobiodon* individuals from our three focal species were collected from their coral colony following the methods of Depczynski and Bellwood (2003, 2004). In short, a weighted fine-mesh (2 mm) conical net was placed around the whole colony before a dilute clove-oil solution (20% clove-oil, 80% ethanol) was sprayed into the net. After 1 min, the net was carefully lifted at the base and anaesthetised individuals of the focal species were collected with hand-held nets and placed into individual zip-loc bags filled with seawater. After all anaesthetised fish had been collected, the colony was extensively searched for any individuals that may have been missed. If there were additional fish present, they were individually sprayed lightly with the clove-oil anaesthetic, with gentle hand movements used to waft the solution over the fish, before they were collected using a hand-held net and placed into another zip-loc bag. Any additional fish within the focal colony were monitored while they recovered and their presence noted if they belonged to the genus *Gobiodon*. The group size of the focal species within each coral colony was recorded from the number of fish collected. In the instance that an individual was sighted within the coral colony but unable to be collected, their presence was added to the focal species group size count. Fish were then taken to shore for euthanasia (UWA AEC permit number: 2024/ET000900).

Fish were then placed in an ice slurry (50% ice, 50% water) to preserve body condition prior to dissection and preservation using 70% ethanol for heads and a histology fixative (FAAC; 4% formaldehyde, 5% glacial acetic acid, 1.3% calcium chloride, 89.7% distilled water) for bodies. All samples were transported to the Coral Bay Research Station, where individuals were counted to determine group size, blotted dry, weighed (to the nearest 0.01 g) and measured across for standard and total lengths, and head, body, and caudal peduncle depths and widths (to the nearest 0.5 mm) (Fig. 2).

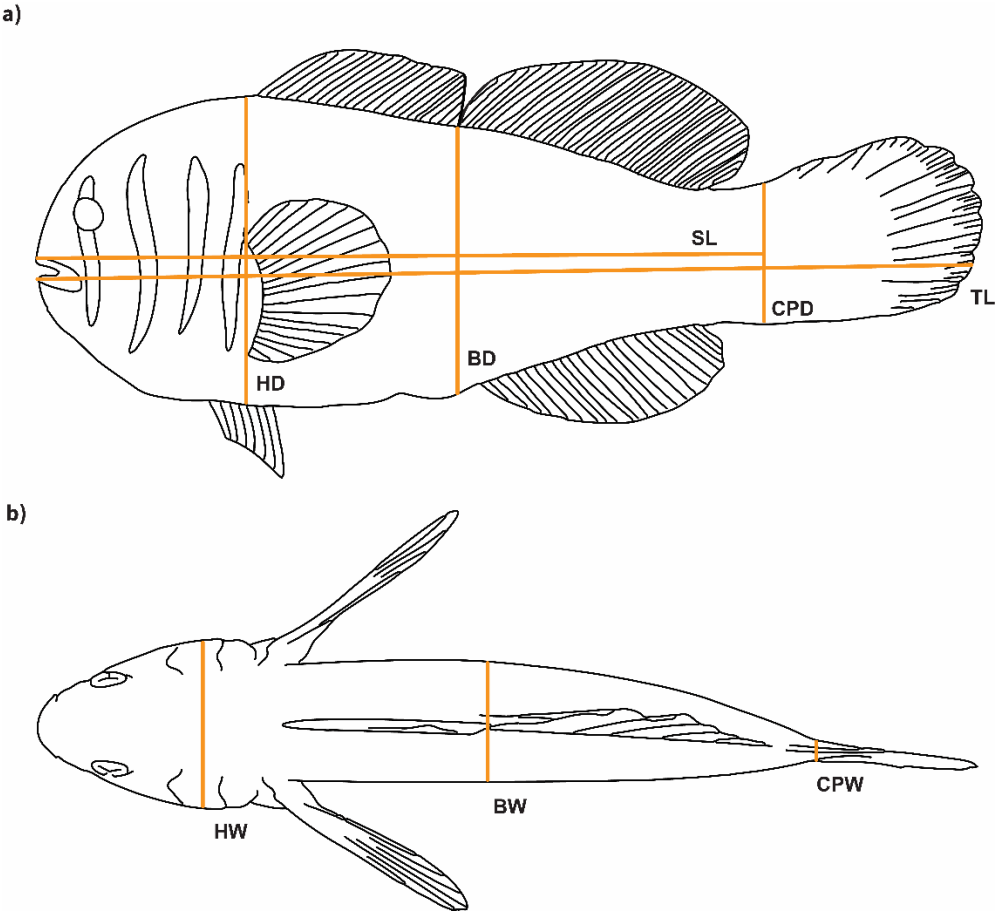


Fig. 2 Morphometric measurements recorded along the longitudinal (a) and ventral (b) sections of each fish. Standard length (SL) was measured from the tip of the snout to the caudal peduncle, total length (TL) was measured from the tip of the snout to the end of the caudal fin. Head depth (HD) and head width (HW) were measured at the deepest and widest points of the head, respectively. Body depth (BD) and body width (BW) were measured at the level of the inter-dorsal space between the first and second dorsal fins. Caudal peduncle depth (CPD) and width (CPW) were measured at the narrowest point of the peduncle. Depth measurements represent dorsoventral distances, whereas width measurements represent lateral distances between the left and right sides of the body. All measurements were taken to the nearest 0.5 mm.

Photogrammetric reconstructions of coral colonies

Three-dimensional models of each coral colony were reconstructed using Agisoft Metashape (Agisoft LLC, version 1.7.6, 2024). Estimates of image quality were made and those with a value of <0.5 were discarded. Photographs were then aligned using the high-quality setting, with a key point limit of 40,000 and a tie point limit of 4,000. Using these alignments, a mesh was produced using depth map construction under ultra-high-quality settings. All meshes were exported in Stanford Polygon File Format and imported into MeshLab (v2025.07; (Cigoni 2008). Here, any surrounding benthic material captured in the reconstruction (e.g. sand, rubble, adjacent substrate) was removed to ensure that subsequent measurements reflected only the coral colony. Next, the number

of vertices and faces were recorded as estimates of model quality (see Supplementary Tables 1-3 for individual model details).

For corals occupied by *G. axillaris* and *G. sp.,* Screened Poisson Reconstruction (Kazhdan and Hoppe 2013) was used to close and account for the spaces between branches that were not accessible or visible for photography. Reconstruction depths of 8, minimum number of samples of 1.5, interpolation weights of 4, and automated orientation of normals were used as the standardised settings across all reconstructions. Any additional reconstructed surface that deviated from the real-world colony (e.g. a reconstructed base below the coral) was subsequently removed, so that the final model most accurately represented the surface of the actual colony. The full structure of corals occupied by *G. citrinus* were visible and captured during *in situ* surveys; however, for consistency with the models where Poisson surface reconstruction was applied, and to ensure the most accurate measurements were obtained, the 'close holes' function was applied to these models.

Each model was scaled using a 30 cm ruler visible in the photographs and incorporated into the reconstruction, ensuring that all geometric measurements were expressed in real-world units (cm). Geometric measures of coral length (cm), width (cm), height (cm), and surface area (cm^2) were calculated in MeshLab. If the ruler had been placed on the benthos or outside the colony, it was removed from the model after scaling. If the ruler remained present in the model, its surface area of 120 cm^2 was deducted from whole-colony surface area measurements.

A convex hull was generated around each coral model using the convex hull function in MeshLab, which produces the minimal convex boundary based on the mesh's vertices, and from which convex hull surface area (cm^2) was derived. Combined with measurements of planar and surface areas, two additional metrics of colony structure were calculated: rugosity and branch packing. Rugosity (Eq. 1) describes the structural complexity of the coral and was calculated as the ratio of coral surface area to planar area (coral length (cm) x coral width (cm)) (Reichert et al. 2017), with higher values indicating greater surface complexity. Branch packing (Eq. 2) describes how surface area is distributed within the three-dimensional space occupied by the colony and was calculated as the ratio of coral surface area to convex hull surface area (Zawada 2019a; Zawada 2019b).

$$\boldsymbol{Eq.\,1.}\ Rugosity = \frac{coral\ surface\ area\ (cm^2)}{coral\ planar\ area\ (cm^2)}$$

$$\boldsymbol{Eq.\,2.}\ Branch\ packing = \frac{coral\ surface\ area\ (cm^2)}{convex\ hull\ surface\ area\ (cm^2)}$$

Statistical analyses

All analyses were conducted in R Statistical Software (R Core Team, 2023). To compare host coral morphology among colonies occupied by *Gobiodon axillaris, G. citrinus,* and *G. sp.*, and to compare adult body morphology among the focal fish species, principal component analyses (PCAs) and descriptive statistics (means $\pm$ standard deviations) were calculated and performed. All variable loadings, the eigenvalue, percentage of variance explained, and cumulative percentage of variance explained for each principal component was recorded (Supplementary Table 4). Coral morphology analyses included all focal coral colonies for each species. Body morphology analyses for the focal fishes were restricted to adult individuals to minimise ontogenetic variation in

body proportions. Species-specific size thresholds were applied to ensure only fully developed adults were included (*G. axillaris* ≥ 32.5 mm SL (n = 33), *G. citrinus* ≥ 35 mm SL (n = 32), *G. sp.* ≥ 30 mm SL (n = 39)). These thresholds were selected conservatively to exclude juvenile and recently matured individuals, ensuring that comparisons reflected interspecific differences in adult body morphology rather than growth-related variation. Prior to PCA, all variables were centred and standardised to unit variance to account for differences in measurement scale. Differences in coral and body morphology were then assessed using permutational multivariate analyses of variance (PERMANOVA) using Euclidean distance matrices and 9,999 permutations. Homogeneity of multivariate dispersion was assessed using permutational analysis of multivariate dispersions (PERMDISP) to evaluate whether dispersion differed among species.

To assess interspecific variation in elongation and lateral compression, we calculated natural-log-transformed ratios of (i) body elongation: standard length to body width (log[SL/BW]), (ii) overall elongation: standard length to head width (log[SL/HW]), (iii) body lateral compression: body depth to body width (log[BD/BW]), and (iv) head lateral compression: head depth to head width (log[HD/HW]). The inclusion of both head measurements was due to the head being both the widest and deepest part of the *Gobiodon* body. Each ratio was compared among species using a one-way analysis of variance (ANOVA), with variation visualised using boxplots.

Group size in relation to coral architecture and health were analysed and plotted separately for each species using generalised linear models with a log-link. Because coral health scores were recorded as ordinal values, its relationship with group size was plotted using boxplots with raw observations. Coral surface area, rugosity, branch packing, and health score were included as predictor variables and standardised within species before model fitting. Because sampling was restricted to occupied colonies, group-size counts could never be zero, and therefore zero-truncated count distributions were used. Zero-truncated Poisson models were fitted for *G. citrinus* and *G. sp.*, while the corresponding model for *G. axillaris* exhibited substantial underdispersion; therefore, a zero-truncated Conway-Maxwell-Poisson distribution, which can accommodate underdispersed counts, was used for this species.

Before model fitting, pairwise correlations among predictor variables were examined separately per species using Pearson correlation coefficients, with $|r| \geq 0.70$ considered indicative of strong collinearity (Dormann et al. 2013). No correlations exceeded this threshold (maximum $|r| = 0.62$), thus no predictors were removed. Variance inflation factors were also examined, with values greater than 5 considered problematic; all VIFs were below this threshold (maximum VIF = 3.28).

Results

Interspecies comparisons of coral host architecture and body morphology

Host coral morphology differed significantly among the three focal *Gobiodon* species (PERMANOVA: $F = 41.66$, $R^2 = 0.547$, $p < 0.001$; Fig. 3a; Supplementary Table 5). The first two principal components explained 92.1% of the variation in coral morphology (PC1 = 73.6%, PC2 = 18.5%). PC1 primarily represented overall colony size, with high loadings for colony length, width, height, planar area, and surface area, whereas PC2 reflected structural complexity, being driven by rugosity and branch packing (Supplementary Table 4). Corals occupied by *G. citrinus* (*A. protoeiformis*) had substantially greater surface area ($\mu = 34{,}904$ cm^2) compared with

G. axillaris (*A. acervata* [μ = 2,802 cm^2]) and *G. sp.* (*A. sp.* [3,997 cm^2]), whereas the latter two species both inhabited comparatively small, densely branched colonies (Fig. 3a; Supplementary Table 6). Consistent with these patterns, pairwise PERMANOVAs showed strong differences between the corals occupied by *G. citrinus* and *G. axillaris* ($R^2 = 0.534$, $p < 0.001$) and *G. sp.* ($R^2 = 0.505$, $p < 0.001$), whereas the corals occupied by *G. axillaris* and *G. sp.* differed only weakly ($R^2 = 0.079$, $p = 0.020$) (Fig. 3a). Multivariate dispersion also differed among species (PERMDISP: $F = 4.15$, $p = 0.014$), with colonies occupied by *G. citrinus* exhibiting greater morphological variation than those occupied by *G. axillaris* ($p = 0.038$) and *G. sp.* ($p = 0.040$), whereas dispersion did not differ between the coral hosts of *G. axillaris* and *G. sp.* ($p = 0.999$).

Body morphology also differed significantly among all three *Gobiodon* species (PERMANOVA: $F = 65.16$, $R^2 = 0.563$, $p < 0.001$; Fig. 3b; Supplementary Table 5). The first two principal components explained 87.1% of the variation in body morphology (PC1 = 79.1%, PC2 = 8.0%). PC1 primarily represented overall body size (e.g. standard length, total length, weight) whereas PC2 reflected variation in body shape (e.g. body and head width, body and head depth) (Supplementary Table 6). Along PC1, *G. citrinus* consistently exhibited greater lengths and weight, and comparisons of univariate metrics align with this pattern (*G. citrinus* maximum SL = 53.0 mm; *G. axillaris*: 41.5 mm; *G. sp.*: 39.0 mm), while along the PC2, *G. axillaris* exhibited proportionally deeper bodies and heads, while *G. citrinus* and *G. sp.* had a comparatively broader body form (Fig. 3b; Supplementary Table 6). Pairwise PERMANOVAs indicated significant morphological differences between all species pairs (all $p < 0.001$), with the greatest separation occurring between *G. citrinus* and *G. sp.* ($R^2 = 0.616$, $p < 0.001$), followed by *G. axillaris* and *G. citrinus* ($R^2 = 0.412$, $p < 0.001$) and *G. axillaris* and *G. sp.* ($R^2 = 0.242$, $p < 0.001$). Multivariate dispersion again differed among species (PERMDISP: $F = 8.22$, $p < 0.001$), with lower intraspecies morphological variation in *G. sp.* than in both *G. axillaris* ($p = 0.012$) and *G. citrinus* ($p < 0.001$), whereas dispersion did not differ between *G. axillaris* and *G. citrinus* ($p = 0.649$).

Relative elongation and lateral compression differed significantly among the three species, whether measured using body or head dimensions (Fig. 4). Standard length relative to body width (body elongation) differed among species ($F = 12.94$, $p < 0.001$). *Gobiodon axillaris* had a higher mean ratio (2.38 ± 0.02 SE) than both *G. citrinus* (2.23 ± 0.02 SE; Tukey-adjusted $p < 0.001$) and *G. sp.* (2.26 ± 0.02 SE; $p < 0.001$), indicating greater elongation relative to width (Fig. 4a). The latter two species did not differ ($p = 0.545$). Standard length relative to head width (overall elongation) showed the same interspecific pattern ($F = 24.22$, $p < 0.001$): *G. axillaris* had a higher mean ratio (2.21± 0.04 SE) than *G. citrinus* (1.92 ± 0.04 SE; $p < 0.001$) and *G. sp.* (1.85 ± 0.04 SE; $p < 0.001$), which did not differ from one another ($p = 0.420$; Fig. 4b). Lateral compression also differed among species at both the body and head. Body lateral compression varied significantly among species ($F = 28.66$, $p < 0.001$), with *G. axillaris* having a higher mean ratio (1.28 ± 0.03 SE) than *G. citrinus* (1.04 ± 0.03 SE; $p < 0.001$) and *G. sp.* (1.03 ± 0.03 SE; $p < 0.001$) (Fig. 4c). The latter two species did not differ ($p = 0.920$). Similarly, head lateral compression differed among species ($F = 43.21$, $p < 0.001$). *G. axillaris* had a higher mean ratio (1.29 ± 0.04 SE) than *G. citrinus* (0.90 ± 0.04 SE; $p < 0.001$) and *G. sp.* (0.78 ± 0.04 SE; $p < 0.001$) (Fig. 4d). Head lateral compression did not differ significantly between *G. citrinus* and *G. sp.* ($p = 0.097$).

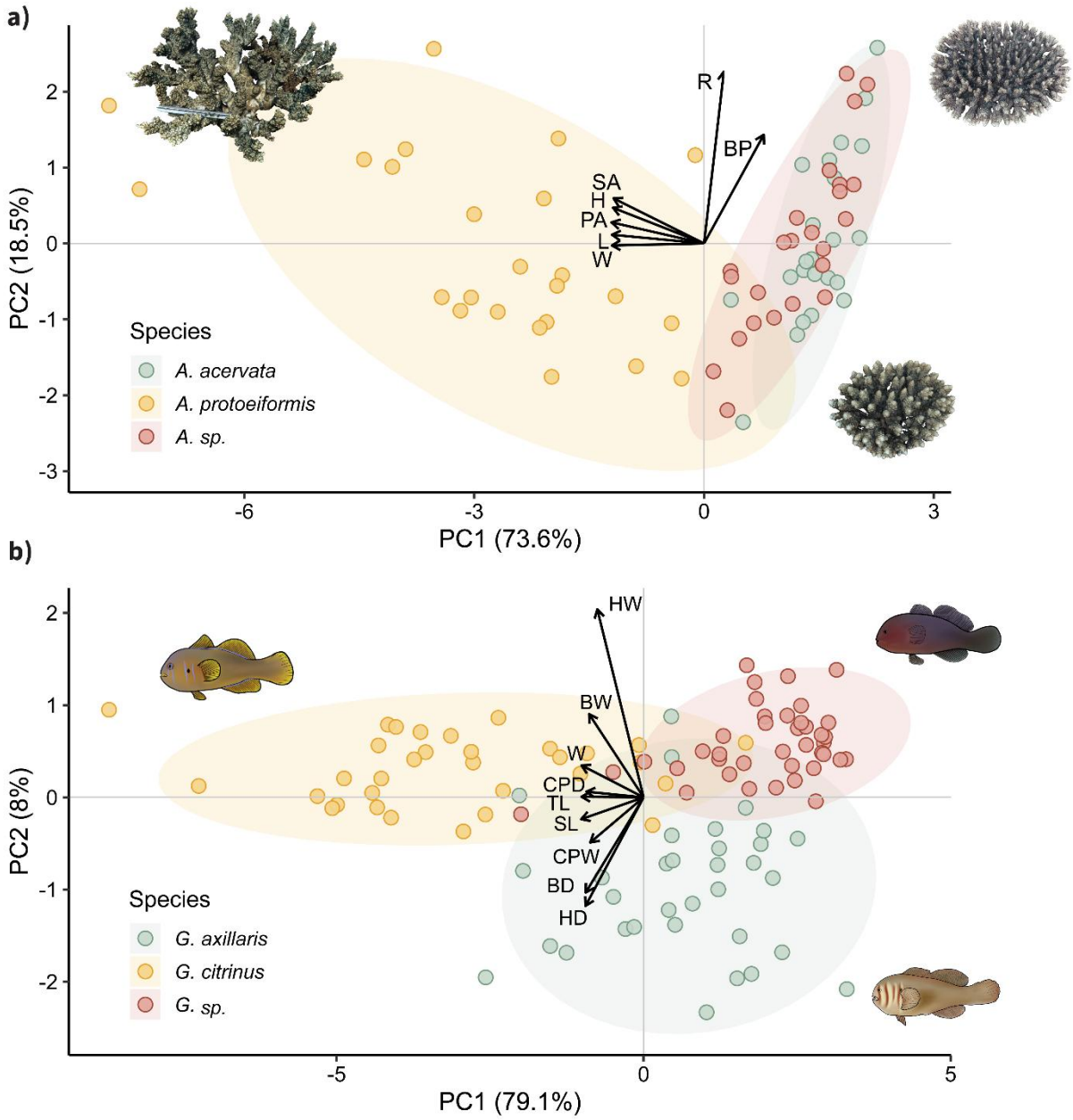


Fig. 3 (a) Principal Component Analyses (PCA) of morphological measurements of coral hosts: *Acropora acervata* (green; *G. axillaris*), *A. protoeiformis* (yellow; *G. citrinus*), and *Acropora sp.* (red; *G. sp.*); L = length (cm); W = width (cm); H = height (cm); PA = planar area (cm^2); SA = surface area (cm^2); R = rugosity; BP = branch packing. (b) PCA of morphological body measurements of *G. axillaris* (green), *G. citrinus* (yellow), and *G. sp.* (red); SL = standard length (mm); TL = total length (mm); HD = head depth (mm); HW = head width (mm); BD = body depth (mm); BW = body width (mm); CPD = caudal peduncle depth (mm); CPW = caudal peduncle width (mm); W = weight (g). Illustrations by Sophie Jones.

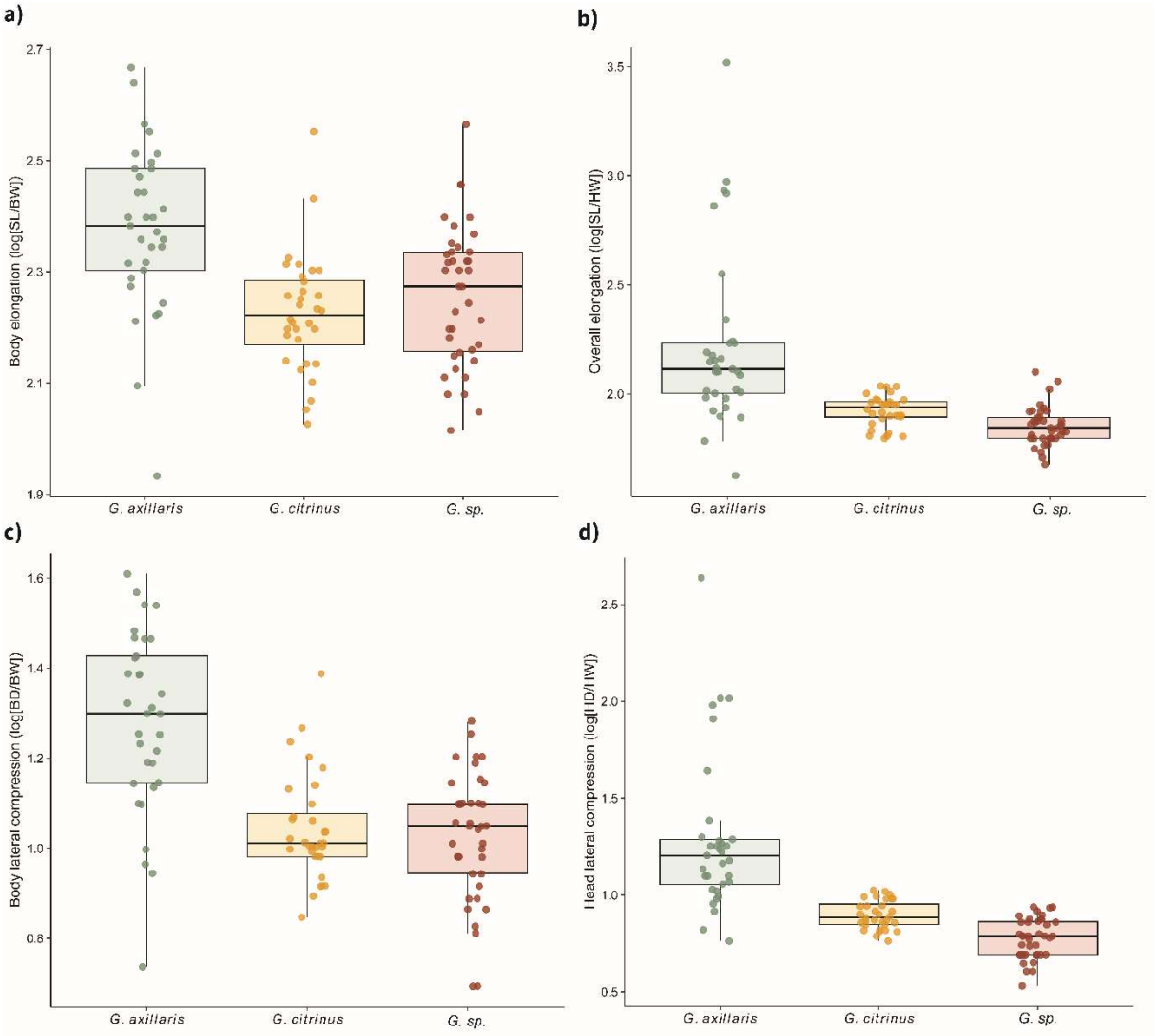


Fig. 4 Variation in (a) body elongation (log[SL/BW]), (b) overall elongation (log[SL/HW]), (c) body lateral compression (log[BD/BW]), and (d) head lateral compression (log[HD/HW]) among *Gobiodon axillaris*, *Gobiodon citrinus*, and *Gobiodon sp.* Larger values indicate greater body and overall elongation (a, b) and greater lateral compression (c, d). Points represent individual fish; boxes show the median and interquartile range, and whiskers extend to 1.5 times the interquartile range. SL = standard length (mm), BW = body width (mm), BD = body depth (mm), HW = head width (mm), HD = head depth (mm).

Group size in response to coral host structure and condition

Coral surface area was positively associated with group size in all three species (Fig. 5a). Group size increased with surface area in *G. axillaris* (ß = 0.201 ± 0.051, z = 3.94, $p < 0.001$), *G. citrinus* (ß = 0.549 ± 0.099, z = 5.55, $p < 0.001$), and *G. sp.* (ß = 0.525 ± 0.145, z = 3.61, $p < 0.001$). These coefficients correspond to expected increases in group size of approximately 22%, 73%, and 69%, respectively, for each one-standard-deviation increase in surface area while other predictor variables remain constant. Group sizes and patterns of host occupancy also differed among species. *G. citrinus* formed the largest groups, reaching a maximum of n = 20 in a single colony,

yet never sharing their hosts with congeners. *G. sp.* formed a maximum group size of n = 11 and often shared coral hosts with other *Gobiodon* species, including *G. histrio,* and *G. okinawae*. *G. axillaris* occurred predominantly in pairs across the observed range of coral surface areas, yet a group size of six was found in the largest sampled colony (SA: 7,421 cm^2).

Rugosity, branch packing, and coral health were not significantly associated with group size in any species when other predictor variables were considered (all $p > 0.077$; Figs. 5b-c, 6). Branch packing showed the strongest, although still non-significant, secondary association with *G. axillaris* ($ß = 0.127 \pm 0.072$, $z = 1.77$, $p = 0.077$). The healthiest coral colonies (score = 6) were occupied by relatively large groups in *G. citrinus* (n = 11) and *G. sp.* (n = 7); however, across all other health scores, group sizes varied, while *G. axillaris* appeared to form similar sized pairings or groups across all levels of coral health (Fig. 6).

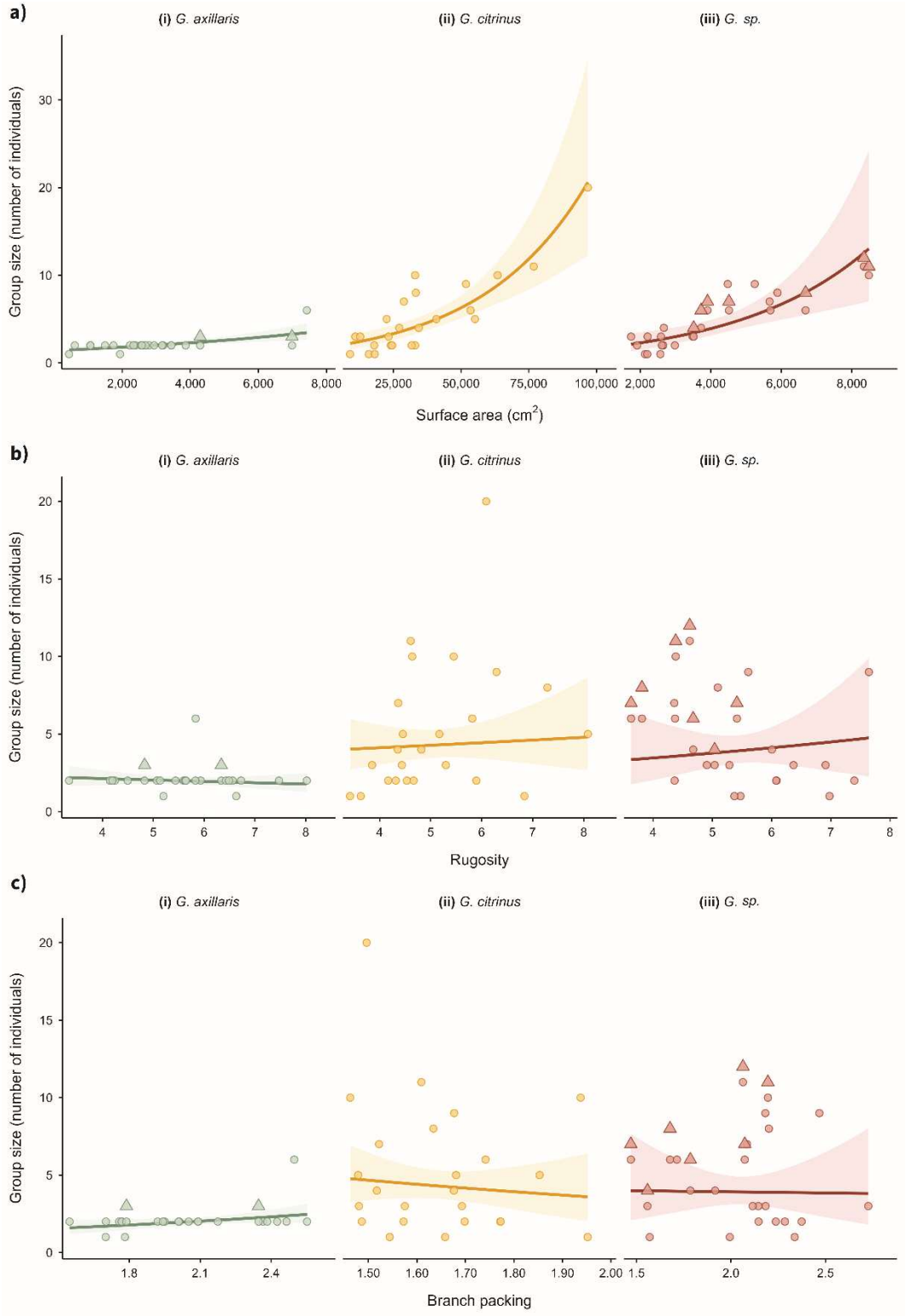


Fig. 5 Focal species group size (circles) and total *Gobiodon* spp. group size (triangles) against (a) coral host surface area (cm^2), (b) rugosity, and (c) branch packing in (i) *Gobiodon axillaris* (*Acropora acervata*), (ii) *G. citrinus* (*A. protoeiformis*), and (iii) *G. sp.* (*Acropora sp.*). Modelled relationships between focal species (circles) and predictor variables are represented by the solid line (±95% confidence intervals). Rugosity = surface area (cm^2)/planar area (cm^2). Branch packing = surface area (cm^2)/convex hull surface area (cm^2).

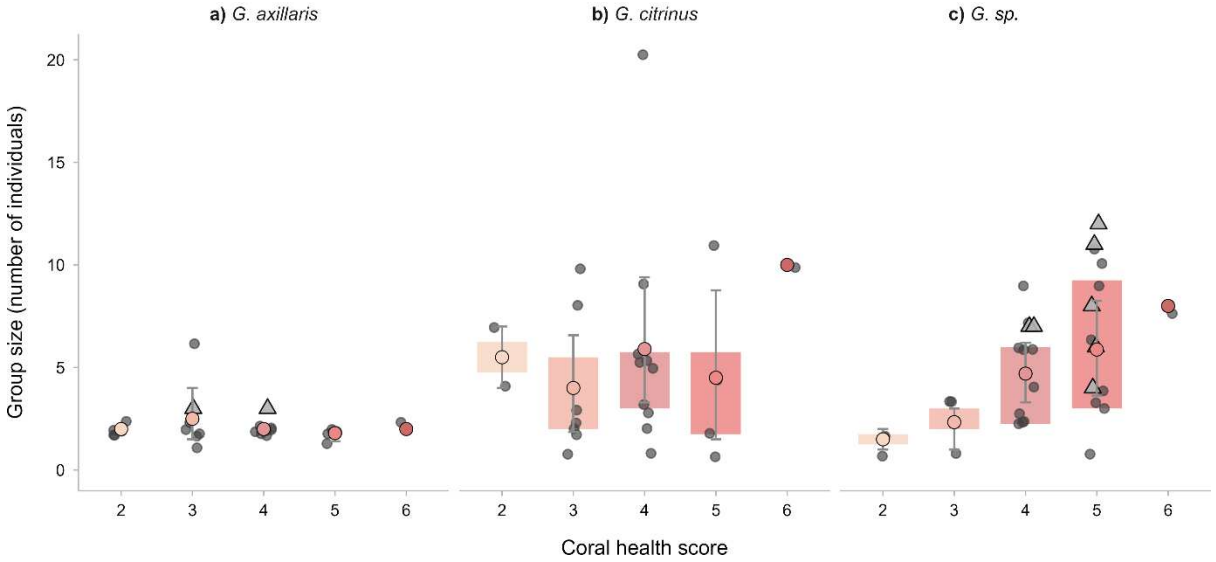


Fig. 6 Focal species group size (circles) and total *Gobiodon* spp. group size (triangles) against the level of health of the hosting coral in (a) *Gobiodon axillaris* (*Acropora acervata*), (b) *G. citrinus* (*A. protoeiformis*), and (c) *G. sp.* (*Acropora sp.*). Coral health was quantified using ordinal health scores from 1 to 6, with lower scores corresponding to lower levels of healthy tissue, and higher scores corresponding to healthier tissue (Siebeck et al. 2006). Boxes represent the interquartile range with median values, points represent individual coral colonies, error bars show mean group size ±95% confidence intervals.

Discussion

Variation in body morphology in relation to coral architecture

The three focal *Gobiodon* species occupied host corals that differed significantly in size and architecture. The clearest distinction occurred between the large, relatively open colonies occupied by *G. citrinus* and the smaller, more densely branched colonies occupied by *G. axillaris* and *G. sp*. These differences were accompanied by substantial interspecific variation in body morphology. *G. citrinus* was the largest species and occupied the largest colonies, whereas the two smaller species inhabited substantially smaller, more densely packed hosts. This suggests that host architecture may act as an ecological filter, determining which body sizes can move through and occupy the available interbranch spaces. Similar associations have been found in other coral-dwelling *Gobiodon* (*G. histrio* and *G. rivulatus*), for which differences in host branch spacing corresponded with variation in body dimensions and maximum body size (Untersteggaber et al. 2014).

Evidence of shape-related specialisation occurred in *G. axillaris*, which occupied highly packed host colonies and was both more elongated and more laterally compressed than the other species. These differences were consistent whether morphology was measured at the body or head: *G. axillaris* had greater standard length relative to both body and head width and greater depth relative to both body and head width. This combination of elongation and lateral compression may facilitate movement between the closely spaced branches of *Acropora acervata*. Wehrberger and Herler (2014) similarly demonstrated that the laterally compressed *G. histrio* can pass through narrower interbranch spaces than wider-bodied *G. rivulatus* of equivalent length. Relationships between

body dimensions and refuge space have also been documented in blenniids, whose body shapes correspond closely to the dimensions of the reef holes they occupy (Wilson et al. 2013). However, *G. sp.* did not differ to *G. citrinus* in either elongation or lateral compression despite occupying smaller, more densely branched colonies. While their standard length to body width ratios are relatively low, *G. sp.* is significantly smaller than *G. citrinus,* allowing them to occupy tight interbranch spacing despite less elongation compared to *G. axillaris.*

While these morphological differences may facilitate movement and occupancy of specific colonies, they may not provide complete protection from predation. Dense branching can increase the availability of refuge for small reef fishes, but structural complexity does not eliminate predation, particularly from similarly elongated or laterally flattened predators (e.g. eels, octopus). For *G. citrinus*, occupying the more open branches of *A. protoeiformis* means exposure to a greater range of predators, including wider-bodied fish. Therefore, their larger body size may offset this predation risk by reducing the number of gape-limited fishes than can predate on them (Mihalitsis et al. 2022). However, body size is also likely to reflect trade-offs involving resource acquisition and competition. Larger body size may allow a competitive advantage when coral colonies are limiting, because competitive rank in *Gobiodon* is strongly size dependent (Munday et al. 2001). Therefore, body size may relate to a trade-off between refuge use and movement within a colony, as well as predator avoidance and group competition.

Collectively, these findings show that contrasting whole-colony architectures are associated with distinct combinations of body size and shape across *Gobiodon*. They are consistent with the hypothesis that interbranch geometry filters the body forms capable of successfully occupying particular host corals (Untersteggaber et al. 2014; Wehrberger and Herler 2014). In particular, the larger-bodied *G. citrinus* is specialised to its larger and more open *A. protoeiformis*, while the elongated and laterally flattened compressed morphology of *G. axillaris* is specialised for movement within densely *A. acervata*. However, the comparatively broad but smaller-bodied *G. sp.* demonstrates that access to confined spaces can be achieved through alternative combinations if body size and shape.

Coral host size as a predictor of group size

Coral surface area was positively associated with group size in all three *Gobiodon* species, indicating that host-colony size places a general constraint on the number of residents a colony can support. This relationship remained significant after accounting for rugosity, branch packing, and coral health, none of which independently predicted group size. Comparable relationships occur in other coral-dwelling *Gobiodon* species (Munday et al. 1998; Hobbs and Munday 2004) as well as other habitat-specialist gobies: group size in *Bryaninops amplus* increases with the available surface area of its gorgonian sea-whip host, *Junceella fragilis* (Jenkins et al. 2024). Larger colonies may support more individuals by providing greater living and breeding space, more refuge from predators and more space over which residents can distribute themselves, thereby reducing competition for shelter (Munday et al. 1998; Hobbs and Munday 2004; Thompson et al. 2007). Because colony size and internal geometry may also change together as corals grow, increasing surface area could be accompanied by longer branches and interbranch spaces that permit occupancy by more individuals or larger-bodied fishes (Untersteggaber et al. 2014; Wehrberger and Herler 2014).

411 The expression of this relationship nevertheless differed among species. *Gobiodon citrinus* and *G. sp.* formed
412 groups of up to 20 and 11 individuals, respectively, whereas *G. axillaris* occurred predominantly in pairs.
413 However, the occurrence of six *G. axillaris* in one of the larger colonies, together with the significant effect of
414 surface area, suggests that this species is not restricted to pairs and that larger hosts can accommodate additional
415 residents. Host size may therefore establish the potential capacity of a colony, while social organisation, mating
416 system, territoriality, and competition may influence how fully that capacity is occupied (Munday et al. 1998;
417 Hobbs and Munday 2004; Munday 2004; Thompson et al. 2007; Chausson et al. 2018; Jenkins et al. 2024). In the
418 predominantly pair-forming *G. histrio*, for example, adults compete for larger host colonies and established pairs
419 strongly restrict the entry of additional individuals (Hobbs and Munday 2004). Similar processes could explain
420 why *G. axillaris* group size increased with surface area but remained lower than that of its more group-forming
421 congeners. In *G. sp.*, which occupy similar-sized coral colonies to *G. axillaris*, larger group sizes may be able to
422 form due to their relatively smaller body sizes, reducing resource use and creating a greater carrying capacity
423 within their coral hosts.
424 Several additional mechanisms could have contributed to the positive relationship between surface area and
425 group size, including recruitment, competition, predation, and food availability. Larger colonies provide a larger
426 target for settling larvae and may contain more food and shelter, increasing both settlement opportunities and post-
427 settlement survival, while resident conspecifics may indicate the presence of suitable resources and act as a cue
428 for settlement (Schmitt and Holbrook 2000; Hunt et al. 2011). Furthermore, resident adults may also indirectly
429 influence post-settlement survival of recruits through their own territoriality of the habitat that reduces overall
430 predation (McCormick and Meekan 2007). Conversely, territorial exclusion by established residents may limit
431 recruitment of smaller or juvenile conspecifics, particularly where a breeding pair can defend the host effectively
432 (Hobbs & Munday, 2004). Predation may impose a further constraint: larger colonies may provide more potential
433 refuges, whereas competition for a limited number of secure interbranch spaces could displace subordinate
434 individuals into more exposed positions and increase their risk of predation (Holbrook and Schmitt 2002). Food
435 availability may also partly contribute to the observed relationship. Although *Gobiodon* consume coral tissue,
436 their corallivory is facultative, and their diets also contain algae, invertebrates, and other material (Brooker et al.
437 2010). Greater surface area could therefore increase the availability of coral-derived food and associated prey,
438 while larger or more exposed colonies may provide greater access to plankton from the water column (Kiflawi
439 and Genin 1997; Finelli et al. 2009).
440 Overall, the consistent relationship between surface area and group size across *Gobiodon axillaris, G. citrinus,*
441 and *G. sp.* suggests that available habitat space is an important determinant of group size, but the number of
442 occupants ultimately reflects interacting effects of shelter, food, recruitment, predation risk, and species-specific
443 social organisation.
444
445 ***Limited response of group size to coral host complexity and condition***
446
447 Neither rugosity nor branch packing independently predicted group size once coral surface area was accounted
448 for. Thus, within the occupied colonies examined, the total amount of habitat provided by a coral was a more
449 consistent determinant of group size than the configuration of its branches.

Habitat size and structural complexity may nevertheless influence different components of habitat suitability. While surface area provides the amount of living space, structural complexity may influence habitat selection, predator access, habitat selection, and the body sizes able to occupy a colony rather than on the total number of residents (Kerry and Bellwood 2012; González-Rivero et al. 2017). Noonan et al. (2012), for example, found that coral branching structure affected habitat selection, survival, and fish size distributions, but responses were not consistently strongest in the most structurally complex colonies. This distinction is also consistent with our findings: branch packing corresponded with interspecific differences in fish size and shape, whereas surface area was the only consistent predictor of group size.

Coral health score was also unrelated to group size across all three species when other size or structural variables were considered. However, raw values illustrated increases in group sizes of *G. citrinus* and *G. sp.* with higher health scores. This suggests that variation in tissue pigmentation among occupied colonies does not strongly influence their capacity to support residents, as long as sufficient living tissue and physical structure remain, with evidence for slight preferences for healthier colonies. Importantly, the absence of a relationship does not demonstrate that coral condition is unimportant for *Gobiodon.* Our study selected occupied coral hosts, disregarding the uninhabited damaged or smothered colonies following the 2024-25 marine heatwave and 2026 Tropical Cyclone Narelle at Nyinggulu Reef. Consequently, the analysis considered variation only among colonies that remained habitable and omitted colonies that may have become unsuitable through bleaching, mortality, or sedimentation. Coral condition may therefore influence whether a colony is occupied before producing a detectable effect on the number of residents within occupied colonies.

Conclusions

This study demonstrates that different components of coral morphology, quantified using three-dimensional photogrammetric reconstructions of colonies, were associated with different aspects of *Gobiodon* morphology and social organisation. Host architecture was associated with interspecific variation in body size and shape: *G. citrinus* occupied large, relatively open colonies and had the largest and broadest body form, whereas *G. axillaris* occupied densely packed colonies and was significantly more elongated and laterally compressed. *G. sp.* achieved occupancy of similarly confined habitats through smaller absolute body size rather than the proportional elongation and compression exhibited by *G. axillaris*. Coral surface area, meanwhile, was the only consistent predictor of group size across all three species. Host size may define the potential ecological capacity of a colony, while species-specific social organisation, competition, and territoriality influence how fully that capacity is occupied.

Three-dimensional photogrammetry provided a robust means of separating the total amount of habitat from its structural configuration, allowing host surface area, rugosity, and branch packing to be quantified at whole-colony scales. Some uncertainty remains because inaccessible colony surfaces cannot be reconstructed and benthic material must be removed manually from the resulting models. Nevertheless, the use of this method in reconstructing the distinct habitats of coral-dwelling *Gobiodon* offers progression in quantifying the surface area and structural complexity of their hosts, allowing us to better understand how fine-scale metrics of coral colonies influence the small-bodied fishes that live within them.

The relationships identified here illustrate how reef degradation may affect coral-dependent fauna through more than the loss of living coral alone. Although structural complexity and health had no detectable effect on group size, disturbances such as tropical cyclones may reduce the size, condition, and surface area of *Acropora* colonies and therefore the number of fishes they can support. Changes in branch architecture may also selectively disadvantage species whose morphology is matched to particular interbranch spaces, such as *G. axillaris, G. sp.,* and other highly specialised coral reef fishes. Consequently, changes in the size and architecture of *Acropora* colonies may affect not only the abundance of coral-dwelling gobies but also their morphological and ecological diversity and the processes of habitat partitioning that facilitates coexistence among species.

Acknowledgements

We first and foremost give our deepest gratitude to the Traditional Owners and first scientists of the sea in which our study was conducted: the Bayungu and Thalanyji people of the Nyinggulu coastline. We thank the Nganhurra Thanardi Garrbu Aboriginal Corporation (NTGAC) for their consent to undertake the fieldwork and fish collections as part of this study. We thank all the incredible volunteers who gave their time, skills, and breath-holds: Teresa Baptista Nobre, Shona Murray, Samantha Crisp, Gina Karnasch, Sophie Jones, Laura-Marie Dehne, Clelia Mulà, Cal Faubel, and Roy Mahon. We further thank Frazer McGregor, at the Coral Bay Research Station, for always looking out for us and keeping us safe. We thank Dr Tom Bridge of the Queensland Museum for providing coral species identification, and Glenn Moore of the Western Australian Museum for sequencing *G. sp.* for species identification.

Funding

This research was supported by the Ecological Society of Australia's Holsworth Wildlife Research Endowment, The Jock Clough Foundation's Robson & Robertson Award, the Forrest Research Foundation, and the Australian Institute of Marine Science. Together, they provided funds and means necessary for data collection in remote Western Australia and software for the production of photogrammetry models.

Competing interests

The authors declare no competing interests.

Ethics approval

All procedures involving animals were approved by the University of Western Australia Animal Ethics Committee under permit 2024/ET000900 and were conducted in accordance with applicable Australian and Western Australian animal-welfare requirements.

Data Availability Statement

The data and code required to reproduce the analyses and results are available at https://doi.org/10.5281/zenodo.22867132.

Author contributions

T. L. J., J. P. E., and D. L. M. conceived the study. T. L. J., M. D., P. J. M. and D. L M. determined the methodologies used for data and fish collections. T. L. J. conducted data and fish collections. T. L. J. produced the photogrammetry models, performed the analyses, produced figures, and wrote the first draft of the paper. All authors interpreted the results and contributed substantially to revisions.

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