REPORT

Microhabitats of sharknose goby (*Elacatinus evelynae*) cleaning stations and their links with cleaning behaviour

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Abstract Coral reefs are renowned for the complexity of their habitat structures and their resulting ability to host more species per unit area than any another marine ecosystem. Dedicated cleaner fish, which acquire all their food resources through client interactions, rely on both the habitat structures (by using topological cleaning stations) and the wide diversity of fish species available on coral reefs, to function. As a result of natural and anthropogenic threats, coral reef habitat structures and their complexity are being lost—despite this threat it is unclear how important reef geometry is to key ecological interactions, like cleaning. Using an established Caribbean reef study site, three-dimensional constructions of discrete coral heads were used to investigate how fine-scale structural complexity traits (structural complexity—measured by rugosity and vector dispersion—height, volume, surface area, percentage live coral cover and refuge availability) relate to cleaner occupancy, abundance and their cleaning interactions with clients. Coral height was a particularly important trait for cleaning, correlating with both the occurrence of cleaning stations on a reef, and with increased cleaning durations and reduced cleaning frequencies/rates. Cleaning stations were also more structurally complex than non-cleaning coral heads, and the increased availability of uneven surfaces (creating cracks and crevices) and refuge availability linked with increased cleaning durations/rates. By understanding habitat features important to cleaner fish on a typical Caribbean fringing reef, we can gain a better understanding of how important reef geometry might be for governing the occurrence and dynamics of such mutualisms.

Keywords Cleaner fish · *Elacatinus evelynae* · Mutualism · Photogrammetry · Structural complexity · Three-dimensional modelling

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Introduction

Coral reefs are renowned for their complex physical three-dimensional structure (termed structural complexity; Graham and Nash 2013). Scleractinia stony corals, which produce hard exoskeletons, are ecosystem engineers, and are largely responsible for the structural complexity of coral reefs (Jones et al. 1994; Wild et al. 2011). Corals' high structural complexity creates a plethora of different microhabitats (Crowder and Cooper 1982), ultimately creating one of the most diverse and abundant habitats in the world (on par with rainforests; Reaka-Kudla 1997). Within a reef environment, different microhabitats influence the spatial distribution of species (Tolimieri 1995) since many species show specific microhabitat preferences (Booth and Wellington 1998; Majoris et al. 2018a), exhibit high site fidelity (Streit and Bellwood 2018) and form close associations with certain microhabitat types (Boström-

Einarsson et al. 2018). However, finer scale variations in coral morphology (e.g. height and substrate heterogeneity) may also promote finer scale differences in species spatial distributions as a result of altered microhabitat—a concept which so far has received little attention in coral reef literature. Since coral structural complexity is under threat from anthropogenic climate change and industrialism (Munday 2004), it is vital to determine the importance of small-scale variation in coral morphology for reef species.

Structural complexity can influence the outcomes of ecological interactions (e.g. predation; Crowder and Cooper 1982; Grabowski 2004, competition; Petren and Case 1998, and herbivory; Vergés et al. 2011), with the magnitude of the effect potentially varying with the degree of complexity (Grabowski 2004). This hypothesis is intriguing and may help further our understanding of the dynamic nature of a classic mutualistic relationship; cleaner-client interactions, which are ubiquitous on coral reefs (White et al. 2007). Cleaning involves a cleaner removing parasites and debris from the body of another species, termed a client (Feder 1966). Dedicated cleaner fish gain all their nutrition from client derived material (formerly termed obligate; Vaughan et al. 2017) and associate strongly with cleaning stations. Cleaners wait at their cleaning stations for clients to visit them, and it has been shown that associating with a cleaning station, rather than wandering across a reef, promotes increased cleaning interactions (Oates et al. 2010; Dunkley et al. 2018). Despite a wealth of knowledge on the ecology of cleaner-client interactions, microhabitat characteristics of cleaning stations are poorly defined. Stations can be cryptic and have been referred to as 'particular ecological situations' (Limbaugh 1961; Youngbluth 1968), which may include corals, anemones or sponges, collection of rocks, and or depressions in the benthos (Limbaugh 1961; Losey 1974; Johnson and Ruben 1988; Sazima et al. 1999; Cheney and Côté 2001; Huebner and Chadwick 2012). Since substrate type can influence the frequency and duration of cleaning interactions (e.g. coral versus sponge; Whiteman and Côté 2002), in addition to the fine-scale distribution, movement, density and diversity of potential clients (Ferreira et al. 2001; Graham and Nash 2013; Ferrari et al. 2018), localised variation in coral morphology may also be expected to influence localised variations in cleaning dynamics.

Traditional methods for quantifying structural complexity, like the chain/tape transect method and Habitat Assessment Scores (Gratwicke and Speight 2005; Wilson et al. 2007) are now being replaced by digital three-dimensional modelling. Such modelling allows for the in silico quantification of habitat complexity traits (e.g. substrate heterogeneity, measured as rugosity and vector dispersion; Storlazzi et al. 2016; González-Rivero et al. 2017; Young et al. 2017, volume and surface area; Ferrari et al.

2017; Raoult et al. 2017, coral cover; González-Rivero et al. 2017, and coral growth; Lange and Perry 2020), which provides finer scale measurements for addressing ecological questions (Storlazzi et al. 2016). Indeed, these techniques have already advanced our understanding on the relationships between varying structural complexity traits and reef fish assemblages (Price et al. 2019) and identified microhabitat types that promote invasive lionfish (*Pterois volitans*) aggregations in the Caribbean (Hunt et al. 2019). The high resolution of such techniques will facilitate the quantification of finer scale variations in coral morphology within a reef environment.
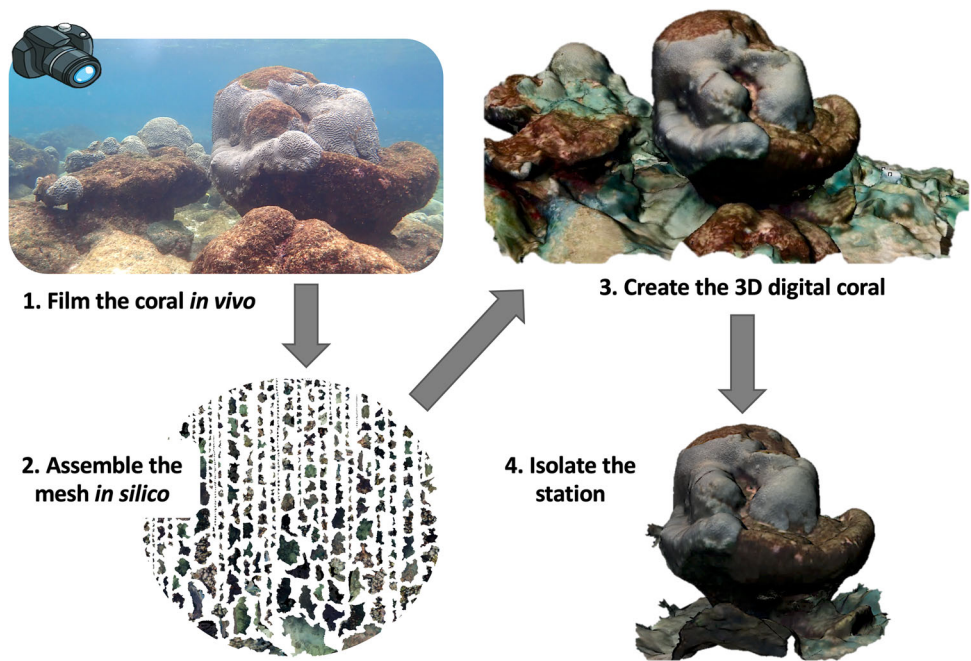
Here, we investigated how different coral morphologies of Faviidae corals, a common group of Caribbean corals, promote variation in the occupancy and cleaning patterns of the predominant dedicated Caribbean cleaner, the sharknose goby (*Elacatinus evelynae*). Using a structure-from-motion approach (Reichert et al. 2016; Ferrari et al. 2017; Young et al. 2017), we constructed three-dimensional models of discrete Faviidae coral heads on a reef in Tobago and quantified different microhabitat traits (e.g. rugosity, height and volume). We then determined whether these different traits distinguished coral heads utilised as cleaning stations versus those that have never been observed as cleaning stations across 8 years of long-term study (see Dunkley et al. 2019b). Subsequently, for cleaning station coral heads, we tested the hypotheses that microhabitat features link to cleaner occupancy distributions and cleaning behaviours (in terms of frequencies, durations and rates). Together, this study aimed to quantify what microhabitat features may define (or not) a cleaning station.

Materials and methods

Study site, occupancy and behavioural observations

The study was conducted on Booby Reef in Man O' War Bay, Tobago (11°19.344′N, 060°33.484′W). The site constitutes a fringing reef dominated by non-branching brain coral species (Faviidae), areas of patchy sand, remnants of dead elkhorn (*Acropora palmata*) and staghorn (*Acropora cervicornis*) corals. For this study, sharknose goby (*Elacatinus evelynae*) cleaning stations were defined as specific localities on the reef used by cleaners for performing their cleaning activities: all cleaning stations were based upon Faviidae coral heads. Corals were not identified to a species level due to the difficulties associated with visual species-level identification (Todd 2008; Forsman et al. 2009). Within a 70 m by 60 m section of the reef, known cleaning station coral heads (from 8 years of long-term study; Dunkley et al. 2019b, *n* = 55 cleaning stations) were marked, along with an additional 12 control Faviidae

Fig. 1 3D digital workflow to show quantification of a control and sharknose goby (*Elacatinus evelynae*) cleaning station coral microhabitat traits on Booby Reef, Man O' War Bay, Tobago: (1) In vivo filming, (2), assembled into mesh chunks in PhotoScan Standard (3) 3D model creation in Rhinoceros 3D (see https://youtu.be/Hy1e0D4USdU) and (4) trim to exclude surrounding reef

1. Film the coral *in vivo*

2. Assemble the mesh *in silico*

3. Create the 3D digital coral

4. Isolate the station

corals. These control corals have never been observed to be occupied by cleaners across 8 years of long-term study at this site (long-term study detailed in Dunkley et al. 2019b).

Cleaner abundance at cleaning stations was quantified using presence/absence surveys ($n = 1549$ surveys, mean $\pm$ S.E. surveys per cleaning station = 28.16 $\pm$ 1.34) over a 6-week period in May–July 2016 by daily snorkelling between the hours of 0830 and 1730 h. For each survey, observers ($n = 6$) searched for cleaners at a marked coral head, and in the close vicinity (~ 2 m^3 area), for up to 2 min—individual cleaners show strong site fidelity to their cleaning stations (Whiteman and Côté 2002; Harding et al. 2003). A cleaner occupancy value was subsequently assigned to each cleaning station—cleaner occupancy was defined here as the proportion of observations where one or more cleaners were present at the station (range: 0–1).

Between presence/absence surveys, data were also collected on the cleaners' cleaning behaviour using 10 min focal observations ($n = 223$ observations, mean number observations per cleaning station across 34 cleaning stations $\pm$ S.E. = 6.56 $\pm$ 0.52, range: 3–13 observations per station). For each observation, stations were randomly sampled throughout the day and one cleaner was randomly selected from their coral head, and we recorded the duration and frequency of cleaning interactions with clients. Cleaning frequencies, durations and cleaning rate were thus used as a measure of cleaning behaviour. The frequencies and durations represent the total effort in cleaning whilst rates represent this effort per cleaning time (i.e. total cleaning frequency/total cleaning duration). Although clients tolerate closer human approaches when being cleaned

(Giglio et al. 2020), snorkelers maintained a 1 m distance from the cleaners during observations.

Three-dimensional digital coral data collection

To create three-dimensional models of the cleaning stations ($n = 55$) and control corals ($n = 12$), video footage was collected with underwater cameras (Olympus GT-4) mounted on monopods, using 1080p resolution and medium sharpness. The physical boundaries of a station were defined as discrete coral head(s) that were not connected to other reef sections (Fig. 1). Filming occurred under ambient light, whilst snorkelling at depths of 1–3 m. At each cleaner station, a cube (6.4 cm^3) was placed adjacent to the coral to serve as a scale. The filming process (adapted from Gutierrez-Heredia et al. 2016) was carried out by swimming slowly, in a spiral motion, starting from the top of the coral and moving down towards the base at the seabed whilst changing the camera angle from (1) top-down (parallel to the seabed), (2) at 45 ° to the coral and seabed, and (3) planar to the coral. To capture fine-scale spatial features of the coral the filming procedure was repeated for each coral head (station and controls) at two different distances: firstly, with the whole coral in full frame, and then, secondly, moving closer (~ 50 cm from the coral). This videoing process was repeated three times for each coral to obtain clear, un-obstructed frames in 360 °, thus accounting for error in videos from obstruction from floating debris and marine life. The duration of each video correlated with the size of the coral head: larger corals were filmed for longer. This created more images for

model reconstruction to ensure quality was not lost as a result of increased coral size. Together, our video recording and processing methods created a standardized approach (e.g. across different coral head sizes and light conditions; Raoult et al. 2017). Video footage was converted to still images using QuickTime™ Player 7.6.6 at an extraction rate of three images per second, resulting in 100–500 images per station with a resolution of 1920 × 1080p. Image sequences were then imported into PhotoScan Standard (Agisoft LLC). Coral models were rendered following the standard workflow sequence in PhotoScan: alignment, dense point cloud generation, mesh building and texture building. Each step was set to medium quality except in the mesh building step where 'meshes maximum face count' was adjusted to 3,000,000 (previously shown to render high resolution models by Young et al. 2017). Final models were compared to still images of corals taken with an Olympus GT-4 camera at four different angles to control for geometric distortion.

Quantifying habitat traits of digital corals

For each coral head (cleaning stations and control coral), we quantified its height (cm), volume (cm^3), surface area (cm^2), linear rugosity (surface roughness/heterogeneity), vector dispersion (another measure of structural complexity; Young et al. 2017), percentage live coral cover and refuge size category. All in silico measurements were recorded using Rhinoceros 3D (Robert McNeel & Associates). Coral dimensions (height, width and depth) were obtained from three-dimensional models using the 'Line' function: to generate distance measures straight lines were drawn (1) down through the centre of the highest point of the coral, (2) across the diameter of the coral, (3) at the widest point and (4) at the narrowest point (using 'DimAligned' function). These measurements were subsequently used to calculate the volume and surface area for each coral, under the assumption that corals represent an elliptical shape (after Adam 2011). Structural complexity was measured with two metrics: linear rugosity and vector dispersion. Linear rugosity chains (2 cm chain link length) were created with a mesh grid with 10 cm spacing using a custom Python script (https://github.com/grace calvertyoung/ Rhino-Python-3D-Coral-Reefs). Using a consistent spacing allowed a standardisation of the number of chains, as all corals were different sizes. Vector dispersion was calculated at a 1 cm resolution following Young et al. (2017). Finally, percentage live cover and refuge size was quantified in situ during video collection using the habitat assessment score (defined in Gratwicke and Speight 2005). For each model, habitat that did not constitute the station (sandy seabed, adjacent rocky outcrops etc.) were excluded using a circumference of 10 cm from the base of the coral (Fig. 1, steps 3 and 4).

Data analysis

Data were analysed in R version 3.4.3 (R Core Team 2017) using Generalized Linear Models (GLMs), Generalised Linear Mixed Models (GLMM, using 'lme4'; Bates et al. 2015) and generalized additive models for location, scale and shape (GAMLSS, package "gamlss"; Rigby and Stasinopoulos 2005). Model assumptions and fits were assessed using residual plots (as specified by Bolker et al. 2009) and all continuous predictors were scaled and centred around zero to facilitate model convergence. Best fitting model selection was based on Akaike Information Criterion (AIC) using a backward elimination approach (with delta < 2). The significance of fixed effects was assessed using likelihood ratio tests comparing models with and without the main effect. The presence of potential influential points on model outcomes were checked for (using Cook's D and leverage), and sensitivity analyses were carried out on identified points (Chatterjee and Hadi 2009): the robustness of results was assessed when identified outlier values were temporarily excluded from models. Significant effects that were sensitive to the presence of influential points are stated in the results.

To determine whether cleaning station corals ($n = 55$) versus control corals ($n = 12$) differed in their microhabitat traits; rugosity, vector dispersion, height, percentage live cover and refuge size category were specified as fixed effects in a binomial logistic GLM (with a probit link). Due to collinearity (identified by Variance Inflation Factor values > 3) between height, volume and surface area, surface area to volume ratio was specified as a main effect (replacing volume and surface area, height still included): this removed any issue with collinearity between variables. It was not suitable to remove any one of these variables from all models or carry out a PCA, since we are interested in the effect of each individual trait.

To determine whether microhabitat traits link with cleaner occupancy (range: 0–1) and abundance (range: 0–9 gobies per presence/absence survey), and cleaning behaviours (frequency, duration and rate), only data from cleaning stations ($n = 55$) were used: this removed false zeros from control corals. Due to further issues with collinearity between height and surface area to volume ratio, we first carried out a sequential regression using these two variables. This method involves regressing the less important variable (in this case specified as surface area to volume ratio) against the other (height) and replacing the less important variable with the residuals from the regression—this disentangles unique from shared contributions from the two variables (Graham 2003). Following
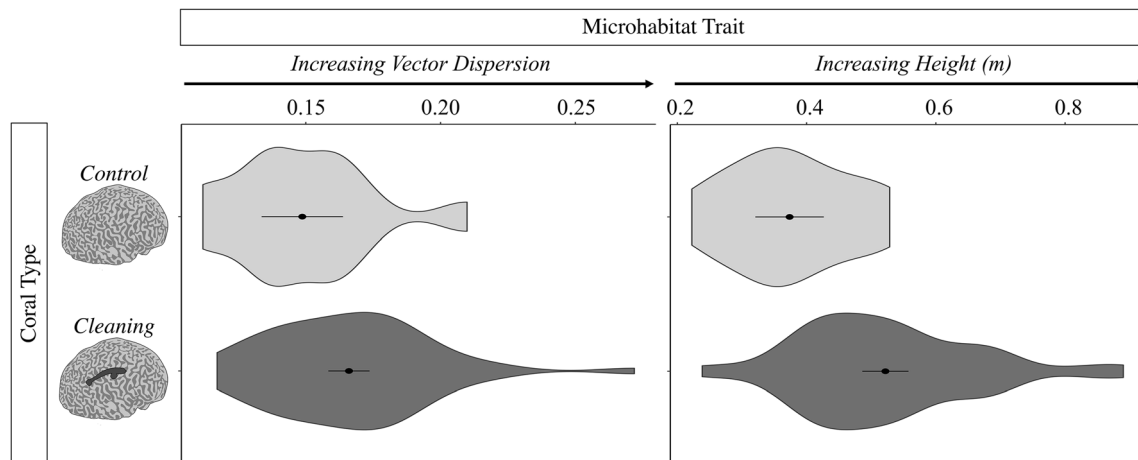
Fig. 2 Microhabitat traits of sharknose goby (*Elacatinus evelynae*) cleaning stations. The outer shapes of the violin plot represent the range of vector dispersions (complexity measure – uniformity in angles of a surface; Young et al. 2017) and heights (m) across cleaning and control corals, while shape thickness shows how frequently these data values occurred. Point and lines show mean ± 95% CI

sequential analysis there was no significant correlation between the variable 'height' and the sequential model residuals. This residual variable was independently calculated for and specified as, a main effect in all further models.

To test for a link between microhabitat traits and occupancy (one value per station); rugosity, vector dispersion, height, surface area to volume ratio residuals, percentage live cover and refuge size category were specified as fixed effects in a Gaussian GLM (with identity link). Prior to analysis, occupancy values were logit transformed since other methods for analysing proportion data (e.g. binomial and beta models) produced poor fitting and overdispersed models (assessed using residual plots). To test for a link between microhabitat traits and cleaner abundance, the same microhabitat traits (including surface area to volume residuals) were specified as fixed effects in a negative binomial GLM. The negative binomial family replaced an overdispersed Poisson model. For this GLM, multiple cleaner abundance counts were aggregated to total amounts per station (following Kratschmer et al. 2018), and an offset was specified, with a log transformation, which accounted for the number of presence/absence surveys per station.

To determine whether microhabitat traits link with cleaning behaviour (frequency, duration and rate) one GAMLSS (for frequency, replacing an overdispersed GLMM) and two GLMMs were specified all with the following fixed effects: rugosity, vector dispersion, height, surface area to volume ratio residuals, percentage live cover and refuge size. Since more than one observer collected behavioural data ($n = 6$), "Observer ID" was included as a random effect in all three models. Data were used on stations ($n = 34$) for which multiple observations

(min $n = 3$) were carried out. For cleaning frequencies, all observation data were included ($n = 223$, contained zeros) whilst for rate and duration, only data containing observations where cleaning events occurred, were included in analyses ($n = 132$ observation, contained no zeros). Cleaning frequency (modelled using beta-binomial GAMLSS, replacing an overdispersed binomial GLMM) and rate (modelled using an inverse Gaussian family with an inverse link) represent the summed interaction frequency/duration for each cleaning interaction within each observation (single value per observation), whilst cleaning duration data (modelled using Gamma family and log link) represented each single individual cleaning event and its respective interaction length (multiple values per observation). Thus, for duration, ObservationID (a unique value assigned to each observation) was also specified as a random effect. The total time for each focal observation accounted for the amount of time a cleaner was out of view and thus varied across observations: for cleaning frequency, values were therefore weighted by observation length. This correction was not necessary for cleaning rate and duration models since their values were independent from observation length. Prior to analysis, cleaning rate values (range: 0.03–1.00) were rescaled from one to ten using the "scales" package (Wickham 2017): this method does not remove the variability between values, but simply transforms data to aid model fit. Finally, to determine whether significant relationships between microhabitat traits and cleaning behaviours were mediated and/or moderated by occupancy/abundance values, station occupancy and cleaner abundance (number of cleaners on the station for each observation) were added to all three final models as individual and interaction terms (occupancy/abundance separately interacted with trait terms). Across

some studies of Caribbean cleaning interactions, cleaning patterns have been shown to vary with time of day (Cote and Molloy 2003; Sikkel et al. 2004, 2005). However, across 8 years of long-term data collected from the same study reef (including data used in this study), Dunkley et al. (2020) consistently found no effect of time of day on cleaning frequencies and durations (as also shown by Grutter et al. 2002; Whiteman & Cote 2002). To avoid overfitting our already complex models, we did not include time of day in our behavioural analyses.

Results

Do cleaning stations show specific microhabitat traits?

Cleaning stations ($n = 55$) were significantly taller than control corals ($n = 12$) and had more structurally complex surfaces (Fig. 2, GLM, $_{model}R^2 = 39.0\%$, height: $\beta = 1.00$, $\chi^2_1 = 11.00$, $p < 0.001$, vector dispersion (uniformity in angles of a surface; Young et al. 2017): $\beta = 0.54$, $\chi^2_1 = 4.13$, $p = 0.042$). Cleaning stations also had lower surface area to volume ratios compared to control corals (GLM, $\beta = -0.62$, $\chi^2_1 = 6.27$, $p = 0.012$) although this result became non-significant when an influential point (relating to a control coral) was temporarily removed ($p > 0.20$). There were no other significant differences between stations and control coral habitat traits (GLM, $p > 0.05$).

Do microhabitat traits link with cleaner occupancy patterns?

Generally, cleaning station microhabitat traits did not predict how frequently cleaning stations were occupied (mean ± S.E. occupancy across stations = 0.56 ± 0.04, GLM, all predictors $p > 0.05$). However, cleaner occupancy tended to increase with the complexity of the coral surface (GLM $_{model}R^2 = 6.1\%$, vector dispersion: $\beta = 0.44$, $F_{1, 53} = 3.42$, $p = 0.070$, $p = 0.033$ when one influential point (station) removed: influential station vector dispersion value = 0.27, mean ± S.E. dispersion value across stations = 0.17 ± 0.004, influential station occupancy = 0.55). Microhabitat traits did not significantly predict the variable abundance of cleaners on stations (GLM, all traits $p > 0.05$, up to nine cleaners occupied an individual station across time, mean cleaner abundance across presence/absence surveys ± S.E. = 0.97 ± 0.03).

### Do microhabitat traits link with cleaning behaviour?

Out of 223 observations across 34 cleaning stations, cleaning was observed 308 times across 132 observations. Cleaning occurred less frequently, and bouts were longer, at taller cleaning stations (Fig. 3, cleaning frequency: GAMLSS, $_{model}R^2 = 5.8\%$, $\chi^2_1 = 5.46$, $p = 0.019$, cleaning duration: GLMM, $_{model}R^2 = 22.9\%$, $\chi^2_1 = 4.58$, $p = 0.032$). Cleaning durations also increased with refuge size category (GLMM, $\chi^2_1 = 4.10$, $p = 0.043$, $p = 0.053$ when one influential cleaning event removed). Cleaning rates, which averaged 0.26 cleaning events per second (± 0.02, S.E.), were lower at taller cleaning stations but increased with structural complexity (Fig. 3, GLMM, $_{model}R^2 = 24.4\%$, height = $\chi^2_1 = 5.97$, $p = 0.015$, vector dispersion = 6.71, $p = 0.010$). Links between cleaning behaviours and microhabitat traits were not mediated/moderated by cleaner presence: generally, cleaning behaviours were not predicted by cleaning station occupancy or the abundance of cleaners, although cleaning frequencies tended to negatively link with occupancy (GAMLSS, $\beta = -0.17$, $\chi^2_1 = 3.45$, $p = 0.063$, height still remained significant when occupancy and cleaner abundance main effects included in model).

Discussion

Here, for the first time, we demonstrate that the cleaning stations of a predominant Caribbean cleaner, the sharknose goby (*Elacatinus evelynae*), can be distinguished from non-station corals by increased height and structural complexity (vector dispersion). Although microhabitat trait variation predicted the occurrence of cleaning stations, they did not predict cleaner occupancy nor abundance patterns of occupied cleaning stations. Variations in coral morphology, however, in terms of height, vector dispersion and refuge size did promote variations in cleaning frequencies, durations and rates. Cleaning events were longer but occurred at a lower frequency and rate at taller corals. Events were also longer when refuge sizes were larger, whilst rates increased with structural complexity (vector dispersion). Together, this study highlights the importance of variation in coral morphology for local cleaner distribution and thus its potential role in moderating the dynamics of cleaning interactions on a larger scale.

Cleaning gobies show strong site fidelity to their cleaning stations (Whiteman and Côté 2002; Harding et al. 2003), are assumed to have short lifespans (mean age documented < 50 days in White et al. 2007) and remain in direct contact with their coral (apart from when cleaning, and the occasional competition-induced move to adjacent coral; Whiteman and Côté 2002; Côté and Soares 2011).

Fig. 3 Sharknose goby (*Elacatinus evelynae*) cleaning station microhabitat traits which predicted their cleaning frequencies, durations and rates. Lines are based on model coefficients (GAMLSS or GLMM) while points represent raw or mean averaged data. Cleaning event values were rescaled from one to 10 to aid model fit. Log transformations were performed for figure clarity. Height, refuge size and vector dispersion are illustrated on a three-dimensional model of one cleaning station from Booby Reef, Man O' War Bay, Tobago
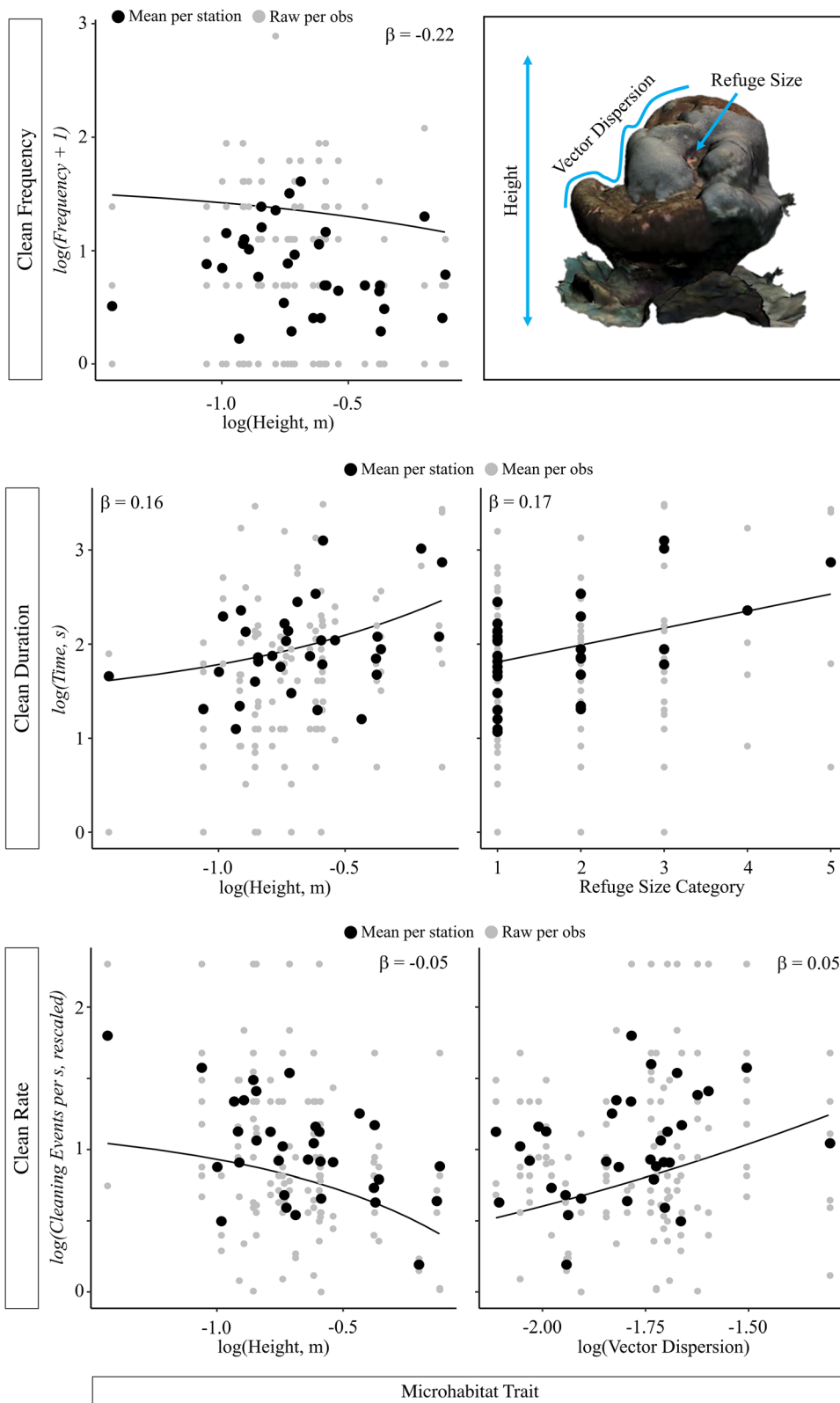
Cleaners adult distribution patterns may thus be, in-part, governed by their larval post-settlement success/settlement site. *Elacatinus* gobies form monogamous pairs (Harding et al. 2003), regularly spawn (*E. evelynae* spawning interval: 9–20 days) and produce high clutch sizes (*E. evelynae*: 200–250 eggs clutch^{-1}, 10–50% survival to

settlement). Importantly, these larvae have lengthy pelagic larval periods (*E. evelynae:* settle 30–40 days post hatching; Colin 1975; Olivotto et al. 2005; Majoris et al. 2018b) and for a closely related species (*E. lori*), larvae have been documented to travel ∼ 2 km from their parent site (D'Aloia et al. 2015). Taller corals which stand above others, may thus 'catch' pre-settlement larvae, whilst increased surface complexity can reduce larvae/adult predation risk (Beukers and Jones 1998; Almany 2004) and alter larval density-dependent mortality once settled (Johnson 2007), together promoting the formation of cleaning stations. However, if our results were simply down to random larvae settlement patterns mediated by their post-settlement survival success, we would also expect coral heads with larger surface areas to also function as cleaning stations (similar to Losey 1974), which was not the case (non-station corals were consistently observed to be unoccupied across 8 years of long-term study; Dunkley et al. 2019b). In addition, although gobies do generally stay affiliated with their coral heads, some localised movements by adults are observed between neighbouring heads (up to ∼ 5 m distance; Dunkley et al. 2019a). Thus, by flexibly moving between corals, adult cleaners may more efficiently increase their fitness by benefitting from differential resources from different coral heads. Choice experiments would help decipher the absolute habitat preferences for this species.

Settlement of coral reef fish in their habitat is complicated, and it is very unlikely that finer scale settlement patterns within an environment are a matter of chance (Victor 1986). Many coral reef fish larvae rely on a combination of cues to control their settlement site selection, including visual, olfactory and acoustic stimuli (Montgomery et al. 2001; Lecchini et al. 2005). It is not clear, however, how sensitive such cues are to finer scale variations (i.e. between corals of the same family as investigated here). Some fish also base settlement cues on the presence of conspecifics and not on the corals characteristics, since the presence of conspecifics could be an indicator of habitat quality (Öhman et al. 1998; Lecchini et al. 2005). This hypothesis is supported for *E. prochilos* (see Whiteman and Côté 2004). However, since density dependence can influence settlement mortality (Johnson 2007), in the current study, we would perhaps expect occupancy/abundance patterns to correlate with microhabitat traits, which we did not observe (in parallel with Wilson and Osenberg 2002, assuming corals are at full carrying capacity, with coral heads assumed to be saturated at very low densities; Whiteman and Côté 2004).

Taller corals also played an important role in influencing the dynamics of cleaning interactions. Investments in cleaning interactions are governed by risk: clients give up foraging time (Grutter et al. 2002) and may be more vulnerable to predators (although both cleaners and clients are thought to be afforded protection to some extent; Cheney et al. 2008; Soares et al. 2012). Cleaning at a taller coral may provide both cleaners and clients with a visual advantage by creating a greater field of view, lowering predation risk (by providing a better view of approaching predators; Nemeth 1998) and facilitating longer cleaning events. Indeed, for a common client of cleaning gobies, *Stegastes partitus* (see Dunkley et al. 2019b), a limited field of view around their territorial site altered their risk-taking behaviour (Rilov et al. 2007). Further exploration of this hypothesis however, will rely on knowledge concerning the visual acuity of cleaner fish and their clients, which is currently unknown (although it is likely to correlate with eye size; Caves et al. 2017). The assumption that station habitat traits that reduce risk and are beneficial for cleaning patterns, can also be supported by our result that longer cleaning bouts were observed at stations with increase refuge size, and that cleaning rates were higher with increased complexity (creating crevices and cracks). Similar to cleaner wrasse (species unknown; Ferrari et al. 2018), here cleaning gobies were found to associate with cleaning stations that showed an increased variation in slopes. The availability of refuges and fine-scale variations in structural complexity (1 cm vector dispersion) may provide a 'safety net' for small bodied cleaners (max 4.5 cm fork length; Cheney and Côté 2003) minimising their risk to threats by reducing access/mobility options for larger predators. Indeed, Ferrari et al. 2018) hypothesized that a strong association with sponges by the sponge-dwelling facultative-cleaning ecotype of sharknose gobies could be explained by the shelter these benthic organisms may provide. It should be highlighted however that if taller corals are more preferable resources (compared to other coral geometries), only gobies expressing beneficial and competitive phenotypes may be expected to dominate such environments, with variation in phenotypes also leading to variations in cleaning behaviour (Dunkley et al. 2019a). Correlating the occurrence of different cleaner behavioural phenotypes (e.g. personality traits) with station microhabitat traits, and their spatial locations may thus be beneficial for future study.

Cleaning patterns can also be governed by the feedback behaviours of their clients (Dunkley et al. 2019a), and clients may use the "landmark feature" of cleaning stations to locate cleaners (Kulbicki and Arnal 1999; Losey 1974) with taller or larger features being easier for clients to locate (Braithwaite and De Perera 2006). In turn, clients may then learn to associate these specific features (e.g. "large spherical corals") with the cleaners (Losey 1974). Indeed, in sparser, heterogeneous environments, organisms tend to aggregate around habitat structures (García-Charton and Pérez-Ruzafa 2001) and thus taller stations may

promote enhanced client numbers/diversity visiting the location—creating foraging choice options for the cleaner. Higher energy gains can be obtained through consuming higher quality foods, feeding for longer and increasing diet breadth (Toscano et al. 2016). Since different clients host species specific parasite assemblages (Grutter 1994), cleaners could maximise their energy loss versus gains by selectively cleaning different client types to optimize their nutrition/energy through fewer interactions. Some client types will be restricted in their spatial distribution on reef by the microhabitat features (Tolimieri 1995) and their reef-use behaviour (e.g. territorial species) however. Taller stations may thus also allow a greater range of 'favourable client types', hosting higher parasite burdens/diversity (e.g. predators, larger body sizes; Poulin and Rohde 1997) to access the cleaner. Incorporation of client functional traits, abundance, diversity, and behaviour data should now thus be considered in future study.

The high structural complexity of coral reefs, which is a defining and vital component of a healthy environment, is under threat from a suite of natural and anthropogenic disturbances (Magel et al. 2019). Here we show that the prevalence and dynamics of cleaning interactions on a local scale, which are also thought to be a vital component of a healthy reef (Clague et al. 2011; Waldie et al. 2011; Demairé et al. 2020), may be vulnerable to even fine-scale changes in microhabitat structure, especially with regards to coral height. Through their large number of interactions with a diversity of client species, cleaning interactions can also drive patterns of fish diversity themselves (Bronstein 2015), playing an important role in the ecological community structure (Floeter et al. 2007; Quimbayo et al. 2018)—changes in the dynamics of cleaning interactions could thus hold strong consequences for the associated reef fish community. It is important to note however, that like all mutualisms, cleaning interactions are highly context dependent: interaction outcomes vary temporally (Cote and Molloy 2003; Sikkel et al. 2004, 2005; Dunkley et al. 2019a, b, 2020) and spatially (Côté 2000; Sikkel et al. 2000; Dunkley et al. 2020; Romain et al. 2020). Whilst we show that microhabitat traits play a role in governing local interaction patterns, a host of additional interlinked contextual factors can influence interaction outcomes (e.g. client identity and abundance; Dunkley et al 2020). It is therefore difficult to determine at this stage, what our findings mean under wide-scale ecosystem degradation scenarios. Compared to the Indo-Pacific, Caribbean reef communities naturally exhibit lower species diversity meaning they are already less resilient to decline and degradation (Bellwood et al. 2004). It is therefore vital that we gain further knowledge of the finer scale habitat requirements of such keystone species in the Caribbean to determine how habitat losses/changes to the reef geometry may both directly and indirectly impact reef communities.

Declarations

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