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Mushroom to manoeuvre? Using photogrammetry to track the movement and survival of free-living corals

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Abstract Mushroom corals can play an important role in tropical reef ecosystems by providing habitat and performing important ecological functions. Unlike most stony corals, free-living mushroom corals can move, both passively and actively, and can use this ability to escape competition or harmful environments. However, as their movement is typically slow, occurs over relatively small scales, and is traditionally hard to measure, their movement ecology is little researched. Nevertheless, quantitative geospatial data on species' movement, distribution, survival, and interaction can improve mechanistic modelling of community dynamics in various environments. We use 'structure from motion' photogrammetry to track 51 individual corals' 3D movement and survival over one year within an isolated and enclosed lagoon. This technique essentially provides a large-scale quantitative community time-lapse and allows detailed individual level life-history data to be collected over spatial and temporal scales that were previously impractical.

Keywords Mushroom corals · Reefs · Movement ecology · Community dynamics · Imaging technology

Introduction

The majority (80%) of Indo-Pacific mushroom corals from the Fungiidae family of stony corals are free-living as adults (Benzoni et al. 2012) and provide habitat and substrate for a range of invertebrate, fish, and algal species (Hoeksema et al. 2012). The Fungiidae can be the dominant component of some tropical reef systems, forming extensive mixed and monospecific aggregations (Hoeksema and Benzoni 2013; Hoeksema et al. 2018). However, reefs are highly dynamic environments, which are affected by human and natural disturbances, such as storms, heatwaves, pollution events, and exploitation at a range of scales. Reef habitats dominated by these free-living corals are therefore generally relatively unstable and transient, and are particularly affected by episodic hydrodynamic disturbances such as storms (Ohara et al. 2021).

While we typically do not think about stony corals moving, the free-living mushroom corals are known to be able to move over small distances to escape competition or harmful environments (Yamashiro and Nishira 1995; Hoeksema and de Voogd 2012) or to be passively swept by storm surge, waves, and strong currents (Ohara et al. 2021). Many species are also able to right themselves following involuntary overturning during such storms (Jokiel and Cowdin 1976; Hoeksema and Bongaerts 2016). Their movement, where recorded, is typically very small scale and at a very slow rate (centimetres to metres per year). Detail on movement is therefore often omitted from ecological research on species such as these with slow or complex life cycles, particularly in the marine environment (Allen et al. 2018). Where movement information is available, it is often restricted in scale, life stage, or location due to the difficulty in collecting adequate metrics. However, having a clearer understanding of species' typical life-history traits and community

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characteristics such as mobility, size–frequency distribution, and survival rate is important for developing ecological models and can usefully inform conservation management (Madin et al. 2016). These trait metrics also help in the understanding of the dynamics of populations and communities over various timescales, or under particular disturbance regimes (Madin and Connolly 2006; Darling et al. 2017; Zawada et al. 2019). The underlying movement ecology, even for extremely slow-paced organisms, helps inform the patterns, mechanisms, and consequences of movement within an environment, and how that effects individuals, populations, community interactions, and their management (Nathan et al. 2008).

Traditionally, the collection of this kind of data for slow-moving mushroom corals is both logistically difficult and laborious, and therefore is typically conducted over a small scale, e.g. 0.25 m² quadrats (Ohara et al. 2021), with a restricted range of metrics collected. However, the development of underwater imaging tools such as ‘structure from motion’ (SfM) photogrammetry now enables researchers to track millimetre-scale changes in reef environments over large areas (> ~500 m²) within a single dive (Bayley and Mogg 2020; Ferrari et al. 2021). Survey locations can then be repeatedly returned to once marked, using photogrammetry to track various changes at the frequency of choice—be it days or years (Magel et al. 2019; Bongaerts et al. 2020; Cresswell et al. 2020).

Here, we use a lagoon site within the Chagos Archipelago with a high abundance of mushroom corals to track the movement of four dominant species (*Ctenactis crassa*, *Fungia fungites*, *Halomitra pileus*, and *Herpolitha limax*) over 1 year. These four species have distinctive features for ID, and cover a broad range of forms, from circular to elongate, and vary in size from small (< 10 cm wide) to large (> 50 cm wide). This broad range of morphologies was selected to be indicative of the diversity of mushroom corals in general within this location. Additionally, the reefs of this study region are very isolated and considered ‘wilderness’ due to the absence of any direct human disturbance (Jones et al. 2018). We can therefore use this remote site to investigate the typical annual rate of mushroom coral movement and survival within a low-energy, sloped environment with no confounding anthropogenic factors. Corals in this region are furthermore generally understudied, particularly within lagoon environments (Hays et al. 2020). This work therefore helps us build a more detailed picture of community dynamics in these isolated systems. We additionally hope that the power of the imaging technique we apply is demonstrated and that the technique can be applied more widely for improving and scaling the collection of such datasets.

Methods

Location

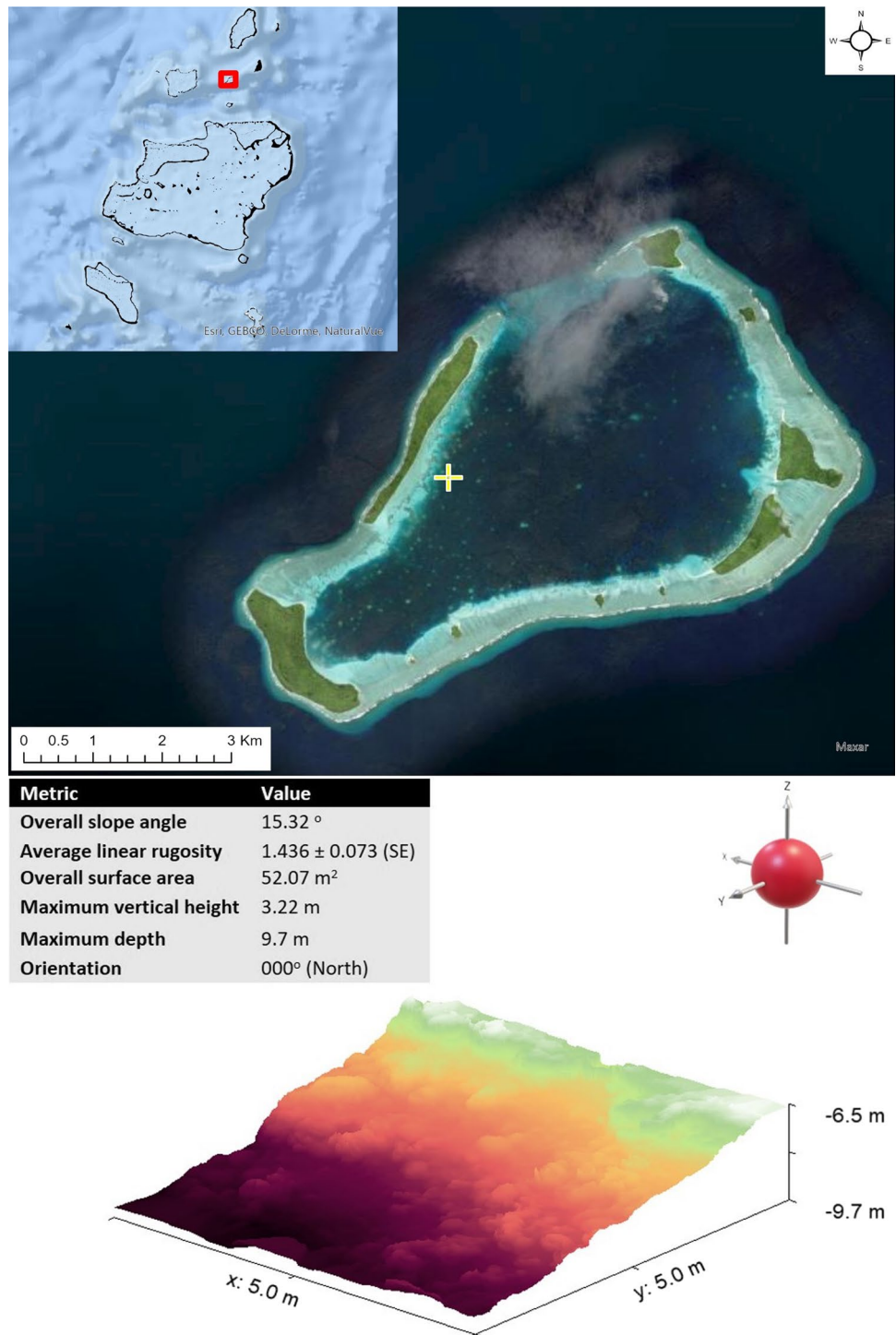
This study was conducted at Sam’s Knoll (Lat/Long: –5.346365, 72.219285), a shallow tropical reef within Salomon Atoll (Chagos Archipelago) in the central Indian Ocean (Fig. 1). The lagoon knoll ranges in depth from ~3 to ~15 m and was surveyed in April 2017 and again in April 2018, at a site marked with permanent GPS-marked rebar stakes. The site is a fully enclosed lagoon with patchy surrounding uninhabited low-lying islands and reef. The site experiences minimal wave exposure or current (except during large storm surge events where waves may pass over the exposed rubble flats) and has no direct human pressures (Hays et al. 2020).

Survey and analysis

The site was surveyed using structure from motion photogrammetry with a single Nikon D750 (24MP) DSLR full-frame camera (with 20 mm wide-angle lens with a dome port). Surveys followed a ‘lawn-mower’ pattern under ambient lighting. Approximately 1000 high-definition images were taken across the reef over an area of ~100 m² and stitched together using Agisoft Metashape (v1.6.3) following the method described in Bayley and Mogg (2020). 3D point-cloud models, digital elevation models (DEMs), and image orthomosaics were calibrated to in situ scale references (for four known point-point distances) and further aligned directly north on a lateral plane using an in situ compass and spirit level for each year. This resulted in a scaling accuracy of 2 mm across each model (with ~80% linear and lateral image overlap), accurate depth (precise to 0.1 m), and consistent 3D orientation. Depth was recorded at the base of a permanent in situ marker at slack water of a neap tide. All Z-plane values within the models were corrected relative to this known depth. Scaled orthomosaics and DEMs were then orientated to a bird’s-eye view and aligned northwards. Once models were aligned, we focused on a 25 m² section of interest that contained a high number of mushroom corals within a restricted depth range.

This section of reef was sloped at a light inclination of 15.32° and ranged in depth from 6.5 to 9.7 m (Fig. 1). The depth range was selected to be small so as to limit this variable as a factor. The section of reef was further selected to be in an area deep enough to have limited exposure to any wave action. The reef is moderately complex, typical of a mixed coral assemblage with a range of colony forms, dominated by mushroom corals (primarily the large, domed *Halomitra pileus*), as well as abundant mid-size tabular *Acropora* spp., massive *Porites lutea*, and *Lobophyllia hemprichii* colonies. Encrusting *Montipora* spp. occurred commonly, and a range of other species were present in small relative abundances.

Fig. 1 Top panel shows the location of the study site within Salomon Atoll, Chagos Archipelago, surveyed in 2017 and 2018. Bottom panel details the 3D reconstruction/digital elevation model of a 5 × 5 m section of the tropical reef knoll, with a north-facing slope. XYZ dimensions and metrics of the surface (slope angle, mean rugosity, total surface area, depth range, and orientation) are also detailed



There are 17 identified species of mushroom coral, from ten genera, within the shallow coral reefs of the Chagos Archipelago (ChIP 2021; WoRMS 2022). A total of four species of mushroom coral were identified within the focus section of reef and included *Halomitra pileus* (n = 28), *Fungia fungites* (n = 13), *Herpolitha limax* (n = 5), and *Ctenactis crassa* (n = 5). All 51 individuals of each species present were digitised within the 25 m² area in 2017 and 2018

using the polygon shapes tool within Agisoft Metashape and exported as shapefiles to QGIS v3.1. Digitisation involved tracing the circumference of each coral based on the calibrated orthomosaic imagery. The circumference of each coral was traced by hand (with a minimum of 20 vertices per coral) and labelled. If an object obscured the coral, this outline was followed unless it accounted for < ~5% of the total shape, whereby a straight line was drawn across

the obscuring object. Each year, the visual condition of each coral was noted (as live, bleached, partial mortality, obscured, or dead). Individual corals were each given a unique ID code in 2017, and corresponding codes were applied to corals in 2018. Individuals in 2018 were identified based on proximity, shape, markings, and size (Supplementary Data).

Within QGIS, centroids were created for each coral polygon, and lateral point-point distances between 2017 and 2018 centroids were created for each coral using the ‘distance matrix’ tool, based on the exported local coordinate reference system (CRS). Depth was calculated for each centroid using the ‘point sampling’ tool, based on the point location over each year’s reef DEM GeoTiff. Lateral area (size) was also calculated for each coral within Agisoft using the ‘measure’ function. Finally, the 3D model of the whole reef section was exported as an XYZ file from Metashape to Gwyddion (Klapetek et al. 2016) for analysis of slope angle and average linear rugosity (10 × 5 m replicates) in order to describe the site’s physical context relative to other reefs. See Bayley et al. (2019) and Bayley and Mogg (2020) for further details of these methods. Population comparisons were conducted using nonparametric Kruskal–Wallis tests and a locally weighted nonparametric smoothing (LOESS) regression. Size–Distance regression was log-transformed to meet assumptions of normality and homoscedasticity. All output data were analysed in RStudio, R version 4.1.1 (R Core Team 2021), using the Tidyverse package.

Results and discussion

Weight and shape differences are known to be important factors affecting movement in mushroom coral species (Hoeksema 1988). The range of annual movement varied between species (Fig. 2a); however, the mean movement was not statistically different ($H_{(3)} = 4.8$, $p = 0.187$, effect size = 0.383). Over the course of the year, the smallest of the mushrooms *Fungia fungites* on average moved the most (Mean = 0.481 ± 0.515 m SD (0.007–1.643 m range)), followed by the larger elongate *Herpolitha limax* (Mean = 0.297 ± 0.195 m SD (0.099–0.540 m range)) and the largest domed species of *Halomitra pileus* (Mean = 0.227 ± 0.355 m SD (0.004–1.528 m range)), with the small elongate *Ctenactis crassa* moving the least (Mean = 0.071 ± 0.045 m SD (0.021–0.124 m range)). The lack of significant mean differences in movement between species may indicate that the predominant driver of movement is local hydrodynamics rather than individual locomotion, in the absence of other pressures. This is further supported by a linear regression of individual size against the total distance moved over the year (Fig. 2d), which showed a negative correlation between size and total distance moved

(Estimate = -0.010 , $F_{1,48} = 12.78$, $p < 0.001$), with the smallest individuals typically moving the farthest.

All individuals moved downslope (i.e. northwards, predominantly NNW) overall over the year (Fig. 2e), except for *Fungia fungites* which had two individuals move slightly shallower upslope (Fig. 2b). This upslope movement was at a depth of 7–8 m, and therefore unlikely to be due to wave action. As with lateral movement, there were no significant differences between species in this sample in terms of downslope movement ($H_{(3)} = 3.27$, $p = 0.352$, effect size = 0.006); however, this may be due to the low-sample sizes of *Herpolitha limax* and *Ctenactis crassa*. Individuals of *Fungia fungites* and *Halomitra pileus* both had outlier individuals move a maximum of ~ 1 m deeper over the year.

Ctenactis crassa and *Fungia fungites* had very similar size–frequency distributions (Fig. 2c), constrained to < 0.5 m², but the analysis shows a much wider size distribution for the larger *Halomitra pileus*, which also occurred at more than twice the abundance of *Fungia fungites* and five times that of the other two species, demonstrating both a greater local abundance and range of ages within this area. While this analysis just assesses a small area of one lagoon, this size–frequency may suggest greater survivorship of these large robust *H. pileus* mushroom corals in the context of the recent severe coral bleaching events in this region (Head et al. 2019).

Over the course of the year, the majority of individuals of each species type survived. However, individuals of *Fungia fungites* and *Halomitra pileus* experienced relatively high proportions of overturning, covering from other organisms or rubble (obscurement), and partial mortality (Fig. 3). Despite the lagoon’s protection from storm disturbance, the overturning of the larger *Halomitra pileus* is suggestive of passive movement from wave surge, and so movement is likely to be a combination of passive and active movement over the year (Hoeksema 1988; Ohara et al. 2021).

While two individuals of *Fungia fungites* were observed to have fully bleached in 2017, these individuals had recovered in 2018. However, while no *Halomitra pileus* individuals appeared fully bleached during the study period (with no recorded large-scale bleaching events in 2017 or 2018), partial mortality was relatively high. Recovery from partial bleaching appeared slow, with no visible change in individuals over the period, potentially highlighting the energetic cost of recovery for this species (Madin et al. 2020). Differential bleaching between species is consistent with similar observations by Hoeksema and Matthews (2011), whereby individuals of the same species may vary in susceptibility according to size and depth. While intraspecific heat–stress tolerance also varies by depth, this greater susceptibility to bleaching in shallower (typically warmer) waters may induce active downslope migration to help reach a cooler environment (Hoeksema 1991; Ohara et al. 2021).

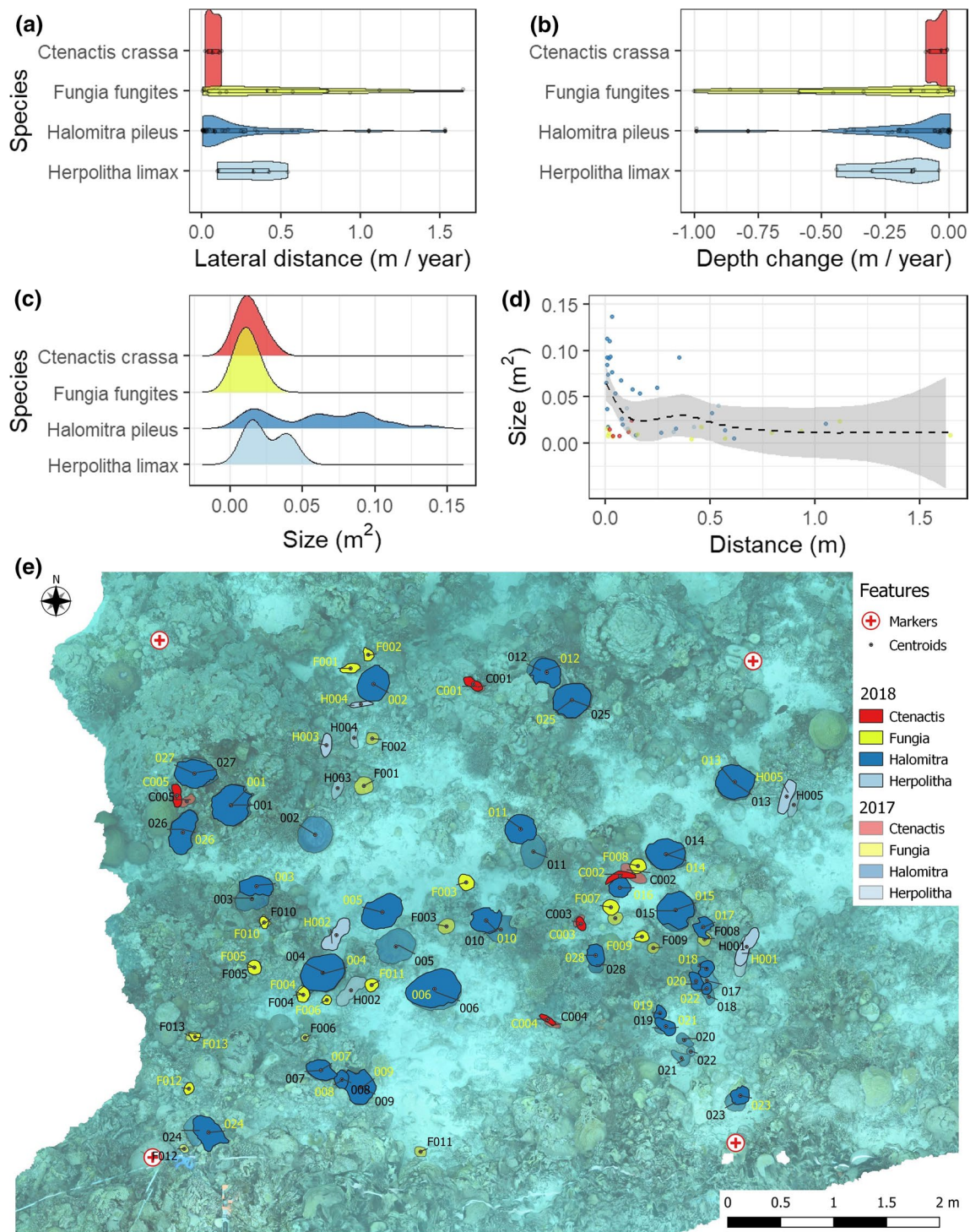


Fig. 2 **A** The lateral point-to-point distances (metres) moved by individuals from four species of mushroom coral over the course of 1 year (April 2017–2018) within an enclosed tropical lagoon; **B** vertical depth change (metres) moved by individuals over the course of 1 year; **C** size–frequency distribution of individuals within the 25 m² surveyed plot; **D** Loess regression of individual coral size against the distance moved over a year ($\pm 95\%$ CI); **E** the start and end locations

of 51 individual mushroom corals tracked over 1 year (April 2017–2018) in Salomon Atoll lagoon, Chagos Archipelago. Black tags (2017), yellow tags (2018), and the four species are highlighted using discrete colours. The background shows the image orthomosaic of the reef knoll in 2017, with ‘markers’ indicating in situ corner references of ~25 m² plot

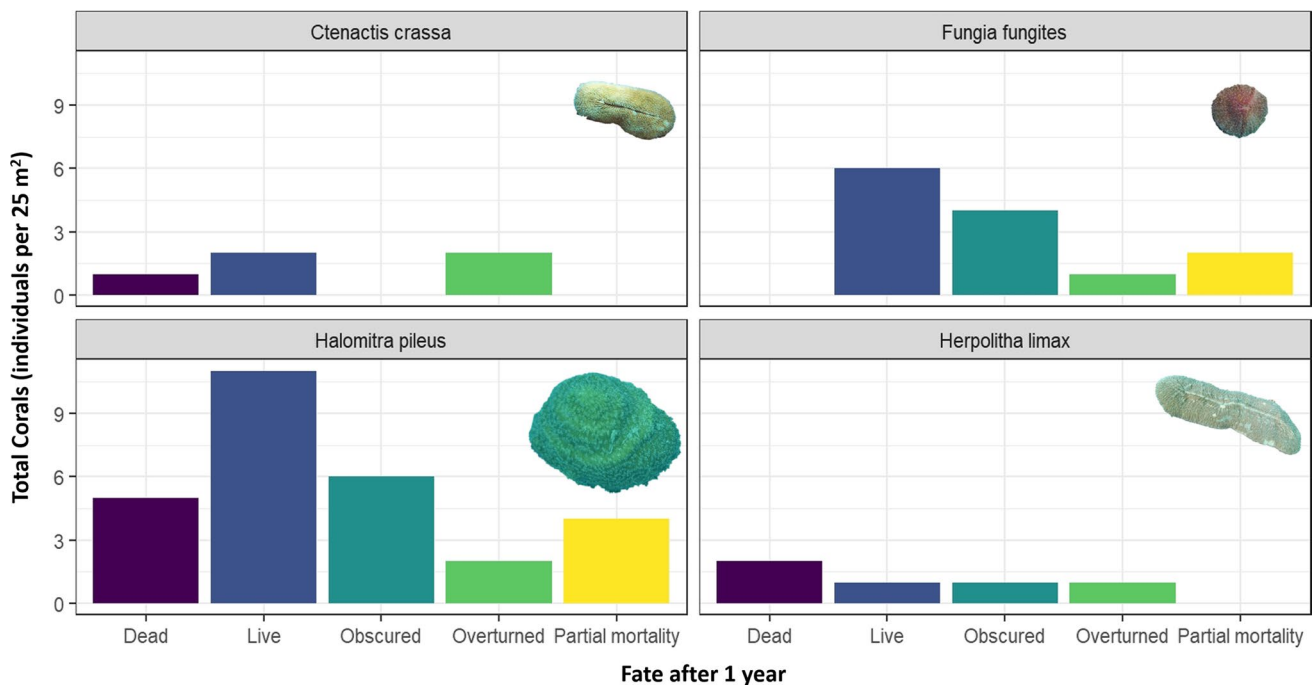


Fig. 3 The overall condition after 1 year (2017–2018) of all individuals from four species of mushroom corals. Individuals were observed within a 25 m² reef plot of an enclosed lagoon in the Chagos Archipelago

Halomitra pileus showed the highest level of mortality and, once overturned, appeared unable to right themselves (making them more susceptible to substrate scour and inhibited feeding). The apparent inability to right themselves is likely due to their large, heavy, concave form, and low initial centre of gravity, which makes returning to an upright position physically far harder (Hoeksema and Bongaerts 2016). In contrast, no mortality was observed in the *Fungia fungites* and all overturned individuals had righted themselves by the 2018 survey, again likely due to their relatively small size and weight. There is a large amount of variation in mushroom corals' tendency to right themselves, according to weight, size, and their environment (Hoeksema 1988; Gittenberger and Hoeksema 2013). However, it is worth noting that smaller, elongate species tend to right themselves more frequently (Gittenberger and Hoeksema 2013), and some, such as young *Herpolitha limax*, can right themselves within a few hours (Hoeksema and Bongaerts 2016). Some overturning and recovery events are therefore very likely to have been missed between survey snapshots in this 1-year frequency study. Similarly, as movement could have been positive and negative in any direction over the year, all total distances recorded, can be considered annual minimums for that individual.

Photogrammetry and 3D digital mapping is rapidly emerging as a very wide-ranging tool for assisting ecological research and management (Bayley and Mogg 2019; Calders et al. 2019; D'Urban Jackson et al. 2020). The ability to

quantitatively assess various processes and precisely monitor change on reefs, will allow researchers to scale up analyses and improve the accuracy of current assessments and future projections. Here, we demonstrate how an area 100 times the size of a traditional quadrat can be analysed to the same level of detail (or 2000 times the size if the entire reconstruction was used). Once permanent markers have been placed in situ (or underwater GPS points recorded), the technique is entirely non-interactive with the substrate, thereby minimising damage and any potential interference. While photomosaics are only one of the outputs possible from SfM photogrammetry (Bayley and Mogg 2020), they are a powerful analytical tool for ecological studies. These mosaics allow a large-scale, spatially explicit record of the reef to be archived in high detail and for the area to be repeatedly surveyed at the frequency of choice. This allows both spatial (e.g. Edwards et al. 2017; Pedersen et al. 2019) and temporal (e.g. Cresswell et al. 2020) ecological patterns to be explored quantitatively and rapidly.

There are of course limitations to the application of this technique and to the tracking of individuals (Bayley and Mogg 2020). For the technique to be effective, accurate high-quality model creation and alignment over time is essential, allowing millimetre-scale accuracy in line with the level of movement of some species. If this accuracy is achieved during collection and processing, the technique becomes very powerful, allowing deeper quantitative analysis of multiple individuals' life-history metrics, and data on

their environment to be recorded. Furthermore, this technique could also potentially be applied to other important benthic organisms or processes on the reef that incorporate passive or slow active movement. For instance, tracking holothurian activity, estimating benthic scour through rubble movement, or quantifying the balance between rubble gain and loss (Wolfe et al. 2021). In this case, tracking the movement of indistinct objects such as rubble could be facilitated by marking individual pieces to improve visibility and recognition.

As this technology progresses, automation of identification and mapping through machine learning is set to become more common, allowing faster or eventually fully automated classification and analysis (Hopkinson et al. 2020; Pavoni et al. 2021; Yuval et al. 2021). For now, the technique outlined allows a previously rarely quantified aspect of coral life-history to be investigated quantitatively over a large scale. This approach allows for a deeper understanding of the spatiotemporal processes and dynamics of such systems, and the slow-moving species inhabiting them.

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