Coral Reefs (2024) 43:1455–1468
https://doi.org/10.1007/s00338-024-02550-4

REPORT

Cushion sea-star removal enhances coral restoration practices and limits background mortality on recovering reefs

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Received: 22 February 2024 / Accepted: 19 August 2024 / Published online: 2 September 2024

Abstract The capacity for natural coral reef recovery and the effectiveness of active restoration efforts are often contingent upon uncertain and understudied background variables, such as chronic predation for example. In the Maldives, small coral colonies (< 10 cm), primarily from the genera *Pocillopora* and *Acropora* (often found recolonising degraded reefs) are frequently predated on by the spiny cushion sea-star (*Culcita schmideliana*). Incidentally, these same corals (especially Acroporids) are often prioritised in active reef restoration practices. However, the level of risk these corallivores pose on restoration success has not yet been assessed. Here, we aimed to initially document the population densities of *C. schmideliana* on a degraded reef system in the Maldives (Kunfunadhoo, Baa Atoll). We then assessed their associated predatory effects on coral recruits and transplants, and explored the benefits of *C. schmideliana* removal on the survival of these corals. Population densities ranged between 1.2 and 3.3 individuals per 100 m^2, which resulted in high predation rates on coral recruits (4 – 20%) and transplants (11 – 43%). *Culcita schmideliana* predation accounted for the majority of the documented mortality (85%). Where *C. schmideliana* were removed, a significant increase in survival for recruits (9% higher) and transplants (24% higher) was shown. Further observations linked a cessation of *C. schmideliana* removal to a significant rise in predation instances for previously protected corals (up to 52%). Our study therefore highlights the severe impacts of *C. schmideliana* predation and shows *Culcita* spp. population management as a viable passive solution for effective reef restoration.

Keywords Coral restoration · Asteroids · Scleractinian corals · Corallivores · Predator removal · Indian Ocean

Introduction

Tropical coral reefs have declined significantly on a global scale, a combined result of several stressors (Ban et al. 2014; Montano et al. 2022a), the most notable of which is arguably reoccurring mass bleaching events (Hughes et al. 2017). Such severe degradation has warranted the rise of coral restoration projects worldwide (Hein et al. 2021; Guest et al. 2023), with the majority focusing on active practices (68%) i.e., utilisation of asexually produced coral fragments (Boström-Einarsson et al. 2020; Randall et al. 2020). These projects often rely on the successful transplantation of small (nursery-grown) coral fragments onto degraded sections of reef (Ferse et al. 2021). Background mortality has always

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-024-02550-4.

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occurred on reefs, but only a few studies have attempted to understand how this aspect impacts reef health under 'normal' conditions (Pisapia et al. 2015). Coral mortality from corallivory for example, may now pose a more severe threat to natural recruitment on reefs following degradation than by other more global stressors (Halpern et al. 2008; Bruckner et al. 2017; Raj et al. 2018; Rice et al. 2019; Bowden-Kerby 2023). Further, such predation on newly transplanted corals may also hinder active coral restoration attempts. This is particularly true in locations such as the Maldivian archipelago, where reefs have been impacted by three major bleaching events, the first in 1998, then again in 2016 and now currently in 2024 (Morri et al. 2015; Ibrahim et al. 2017; Saponari et al. 2018; Montano et al. 2022b; Sweet, 2024 *pers obvs*). Coral cover in this region is now estimated to be less than 20% (on average)—with slow growing taxa such as *Porites* now dominating many reefs (Montano et al. 2022a). As a result, the majority of active restoration programs focus on increasing coral cover through the propagation and transplantation of fast-growing, branching coral, namely Acroporids and Pocilloporids (Pisapia et al. 2019; Boström-Einarsson et al. 2020; Ferse et al. 2021; Guest et al. 2023). Incidentally these are the same taxa which are the preferred food source of many corallivores like cushion sea-stars (*Culcita* spp.) (Montalbetti et al. 2022) and the crown-of-thorns starfish (*Acanthaster* spp.) (Johansson et al. 2016; Pratchett et al. 2017).

There is an abundance of research on *Acanthaster* spp. (Rotjan & Lewis 2008; Pratchett et al. 2017; Montano et al. 2022a) but less so on *Culcita* spp. (Bruckner & Coward 2019; Montalbetti et al. 2019). Both are commonly encountered on reefs throughout the Maldives with *Acanthaster* historically occurring in 'plague' proportions hitting densities of approximately 361 individuals per hectare (Saponari et al. 2018). However, the abundance of *Culcita* spp. has to date not been assessed sufficiently. Some taxonomic uncertainty also exists of Maldivian *Culcita* spp., for example there are unclear delineations of a certain morphological feature, namely the size and position of 'paxillae' located on the derma-skeleton, an indicative feature found in both the spiny cushion sea-star (*Culcita schmideliana*) and the more Pacific based *Culcita novaeguineae* (Moosleitner 1990). However, currently the literature only supports identification of *C. schmideliana* in the Maldives, and therefore we refer to Maldivian *Culcita* sp. as *C. schmideliana* from here on out (Montalbetti et al. 2018). *Culcita* spp. feed in the same manner as *Acanthaster* spp. (Thomassin 1976) i.e., eversion of their stomach and the subsequent release of digestive enzymes (Montalbetti et al. 2018). Although it is recognised that they have a varied diet, both species of *Culcita* exhibit a distinct proclivity toward coral (Glynn and Krupp 1986; Montalbetti et al. 2018; Bruckner and Coward 2019). For example, *C. schmideliana* is recorded to feed on at least 12 hard coral genera with a marked preference for *Pocillopora* (51%) and *Acropora* (21%) (Bruckner and Coward 2019). Interestingly, the round anatomy of *Culcita* spp. and their lack of prehensile arms, means that unlike *Acanthaster*, the feeding niche of *Culcita* spp. is restricted to small colonies, fragments, or peripheral and protruding branches of larger corals that their oral surfaces can mount (Goreau et al. 1972; Glynn and Krupp 1986). Indeed, they appear to have a feeding niche which favours recruits and juvenile colonies < 10 cm (Glynn and Krupp 1986; Bruckner & Coward 2019; Montalbetti et al. 2019). The implications of this particular diet, especially on degraded reefs, poses an issue and indicates *Culcita* spp. predation may be a relatively unknown threat which could be limiting active coral restoration effectiveness. Passive restoration efforts in contrast – i.e., those which focus on the removal of affecting factors such as corallivores in this case, may be one way to improve reef health at local scales (Gann et al. 2019; Boström-Einarsson et al. 2020). Moving forward, reef practioners therefore may need to consider tailored restorative projects, utilising a combination of both passive and active restoration techniques (Possingham et al. 2015).

Research on normal population densities of *Culcita* spp. in the Indo-Pacific is limited (Quinn & Kojis 2003; Pratchett et al. 2011). Populations of *C. schmideliana* have typically been considered rare (< 0.5 individuals per 100 m^2), but recent publications in Raa and Faafu Atoll within the Maldives archipelago have reported 'outbreak' densities of up to 9.2 individuals per 100 m^2 (Bruckner and Coward 2019; Montalbetti et al. 2019). However, even 'normal' densities of *Culcita* spp. appear to have exacerbated effects on degraded reefs due to imbalanced predator–prey relationships following large-scale loss of coral cover after major disturbances (Raj et al. 2018). In addition, unrelenting and selective predation by *Culcita* spp. are likely limiting the adaptive capacities of resistant generations of coral communities experiencing sequential bleaching events (Bowden-Kerby 2023).

Asteroid (and gastropod) population management has certainly been adopted as a viable passive restoration technique in other regions like Australia and Malaysia (Shafir et al. 2006; Rotjan & Lewis 2008; Williams et al. 2014; Nakamura et al. 2016; Pratchett et al. 2017; Chak et al. 2018; Shaver et al. 2018; Westcott et al. 2020; Kroon et al. 2021). Although *Culcita* spp. research in general is very much in its infancy, early studies have suggested *Culcita* spp. control may benefit reef recovery and coral restoration efforts (Quinn & Kojis 2003; Bruckner & Coward 2019; Montalbetti et al. 2022). Some localised culls have recently been carried out in the Maldives (Zahir et al. 2010), but there have been no quantifiable measures that test the combination of *Culcita* spp. control with active coral restoration in this region (or elsewhere for that matter).

In 2021, a large-scale restoration project began at Kunfunadhoo Island, in Baa Atoll. Primary methods for restoring the reef include rearing coral within a series of *in-situ* and *ex-situ* nurseries and transplanting asexually propagated fragments onto the degraded 'house-reef'. This has more recently been supplemented by sexually produced coral larvae, reared to transplantable size. The project utilises multiple propagation techniques, including mineral accretion technology (Goreau 2012), micro-fragmentation (Forsman et al. 2015), rope nurseries (Dehnert et al. 2022), corals of 'opportunity' collection and transplantation (Monty et al. 2006) and *ex-situ* coral spawning and rearing (Craggs et al. 2017). *Acropora* and *Pocillopora* respectively equate for the majority of transplanted coral taxa, with corals usually ranging between 5 and 10 cm in diameter when transplanted. Initial personal observations during transplantation indicated that survivorship was low and the majority of death was attributed to predation by *C. schmideliana*.

This study therefore aimed to determine population densities of *C. schmideliana* at several restoration sites and the associated predation trends on transplanted fragments, as well as naturally recruited coral. We then experimented with the removal of *C. schmideliana* and measured the impact this had on coral survivorship. The overall aim of this research was to test and outline a stand-alone passive tool for natural reef recovery, and also one that could be utilised to supplement active coral restoration approaches throughout the archipelago, and perhaps beyond.

Materials and methods

Study sites

This study took place between March and December 2023 on Kunfunadhoo Island (5.1120°N, 73.0780°E) within Baa Atoll, Maldives, a UNESCO Biosphere Reserve. Here, restoration projects run by Coralive and the Soneva Foundation Science and Conservation team (Soneva Conservation and Sustainability Maldives) have been operational since 2021. Kunfunadhoo is 0.42 km^2 with a reef encompassing the entire periphery of the island. The majority of the reef (north, south, and west facing) consists of a small reef flat/lagoonal zone (depth 1 – 2 m) made up of rubble and sand. Soon after this, a shallow reef crest descends down a sloping fore-reef (2 – 4 m) consisting of hard coral cover, deceased coral heads and rubble patches, into a steep wall that flattens out between 20 and 30 m. The eastern side of the island, which faces the edge of Baa Atoll, is made up of a large lagoonal area that leads to a reef crest with a deeper sloping fore-reef (3 – 7 m) that also descends into a steep wall. The Maldives is subject to seasonal weather variations, with predominant wind and current directions steered by the south-west monsoon from May to November and north-east monsoon from January to March (Stevens and Froman 2018). Five study sites of comparable benthic composition and depth on the reef were selected to carry out experiments, with all sites located on flat, shallow (depth 1.6 – 5.8 m) fore-reef made up of hard-coral cover and limestone rubble (Fig. 1). The sites were named 1) 'Out of the Blue Right' ('OOTB R') (mean depth 2.2 m; 2) 'Watersports' (mean depth 2.4 m); 3) 'Out of the Blue Left' ('OOTB L') (mean depth 2.9 m); 4) 'Out of the Sea Left' ('OOTS L') (mean depth 1.8 m); and 5) 'Nursery' (mean depth 5.8 m). All sites except 'Nursery' were accessible from shore. Treatment plots within these sites were at similar depths to each other (± 0.4 m).

Population assessments of *C. schmideliana*

To determine population densities of *C. schmideliana* around the island, each site was randomly surveyed 12 times using a standard 50 × 4 m transect (200 m^2) (Montalbetti et al. 2019). These surveys were undertaken on the fore-reef (1.1 – 7.2 m depth) between November 2022 and November 2023. All sampling time-points were randomly chosen within this timeframe. This does mean (and it is acknowledged) that we unfortunately did not continually monitor the same site each and every month, and therefore were unable to ascertain any shift or variation in population dynamics over time in this current study. That said, transects were laid randomly within sites and never laid in the same area within the same month in order to avoid pseudo-replication of data. Transects were also not laid in areas where *C. schmideliana* removal/relocation occurred. Presence of *C. schmideliana* was recorded visually, with individuals not interfered with. Surveys were carried out by pairs of divers, each investigating 2 m on each side of the transect line. The resulting survey-specific search area was set at 4 m width along the central line of the survey path. The pairs of divers therefore remained on each side of the transect line to further avoid pseudo-replication of observations. Due to the obscure diurnal nature of *Culcita* (Glynn and Krupp 1986), surveyors were required to methodically search within the transect area, with careful attention to small crevices and under boulders and rocks, this was in addition to any conspicuous habitat also encountered. However, due to this cryptic nature reported, densities should be considered as conservative estimates (Glynn and Krupp 1986). Presence of *Acanthaster* were also recorded if/when encountered.

Experimental design

To test the effect of *C. schmideliana* removal on coral predation, the following experiment was conducted. Each of the five sites contained two treatment plots: a control (*C.*

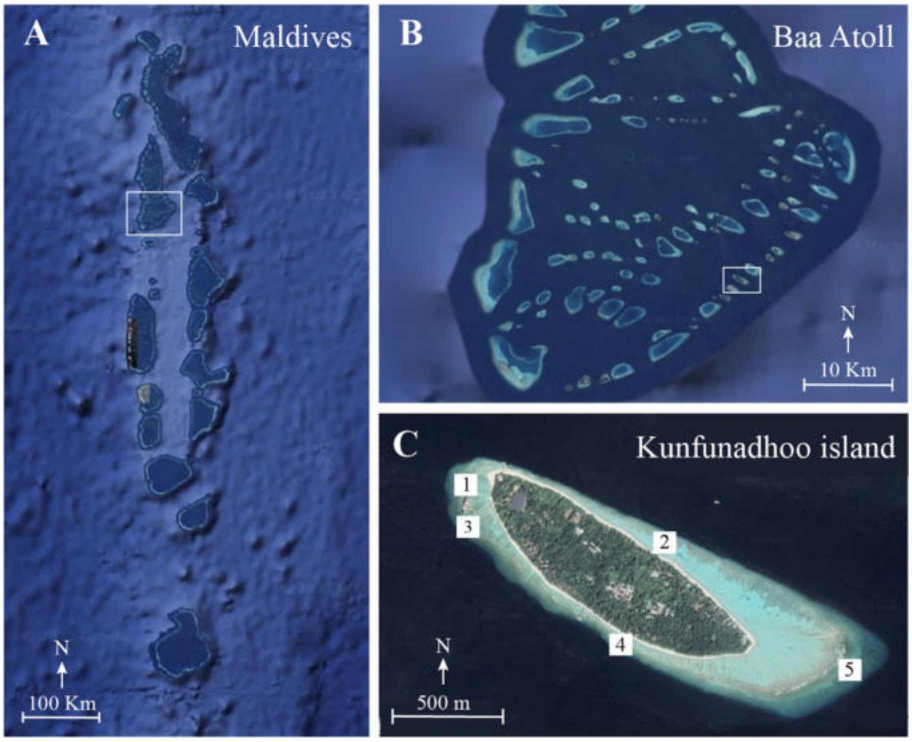

Fig. 1 **A** Satellite image of the Republic of Maldives. **B** Location of Kunfunadhoo Island in Baa Atoll. **C** Image of Kunfunadhoo Island with associated study sites on the reef: 1) 'Out of the Blue Right'; 2) 'Watersports' 3) 'Out of the Blue Left'; 4) 'Out of the Sea Left'; 5) 'Nursery' (Google Maps 2023)

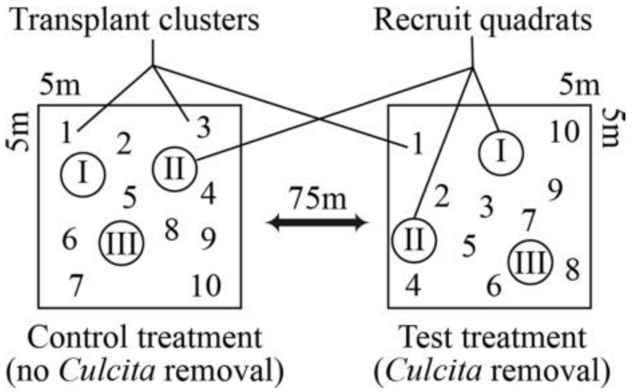

Fig. 2 Experimental design of the two treatment plots located at each survey site

schmideliana not removed) and a test treatment (*C. schmideliana* removed) (n = 5 per treatment). Distance between treatments was measured at 75 m apart to account for spatial autocorrelation owing to the removal and relocation of *C. schmideliana* in test plots. This is justified by the slow-moving nature of *Culcita* spp. (Glynn & Krupp 1986; Montalbetti et al. 2018). 25 m^2 quadrats were marked using rope elevated off the seabed and secured by steel nails to visualise the plots within sites (Fig. 2). Within each treatment plot, points on a range of accessible flat surfaces were marked with coloured numbered tags, and at each tag, a cluster of 10 coral fragments were transplanted using cement as the adhesive. In each treatment plot, a total of 50 *Acropora* spp. fragments and 50 *Pocillopora* spp. fragments were transplanted. Coral fragments were selected from relocated donor colonies originally from Gulhi Falhu, a development island near Male. Small fragments (~ 7 cm) were cut from these colonies, representing the typical size range for transplanting corals on Kunfunadhoo. In each treatment plot, only one genotype of coral for each genus was selected as the source of the fragments. Fragments from whole colonies were cemented sporadically within an approximately 0.25 m^2 area around the cluster tag.

Natural coral colonies under 10 cm from the same two genera (the preferred food choice of *C. schmideliana*) were also monitored over the experimental period (Glynn and Krupp 1986; Montalbetti et al. 2019). Three coloured numbered tags were installed to mark the centres of invisible circular quadrats (3.14 m^2) within each treatment plot, that were sampled using a 1 m line extended from the central nail and rotated (Nicolai et al. 2008).

In total, 1000 corals were transplanted into the clusters (100 corals in each treatment plot). In addition, 973 natural colonies (465 in control plots and 508 in test plots) were monitored within the fixed circular quadrats (across all sites and plots). Sites ran in two different time periods due to operational restrictions and limited staffing, but all sites ran for nine weeks. 'OOTB R' and 'Watersports' were set up and monitored from March – May 2023, and 'OOTB L', 'OOTS L' and 'Nursery' ran from June – August 2023. To minimise the impact of expected initial mortality and failed attachment of corals during the transplanting phase, and to maximise observed *C. schmideliana* predation across equal sample sizes, all sites underwent three maintenance dives prior to the initial week of data collection. Loose or dead fragments over a week-long period were replaced by fresh fragments from the same donor colony and cemented in missing locations.

Culcita schmideliana removal at test sites

The test treatment plots (within each site) were subjected to predator removal of *C. schmideliana* (permit number: PA/CN-CR/2022/01). This occurred twice a week under a standardised and consistent protocol by pairs of divers on SCUBA. Searches were timed to 45 min per plot. Searches began with an initial search covering the entire 25 m^2 marked plot. This was then followed by a spiral search pattern extending to 20 m either side of the plot, making up an area of 2025 m^2. Divers would swim laterally, covering 2 m either side of a transect line that increased at 4 m increments with every lap of the area. *Culcita schmideliana* are cryptic in nature (Glynn and Krupp 1986), and as such, searches required scrutiny with particular attention to inconspicuous habitats underneath coral heads and in-between crevices. Any *C. schmideliana* observed within the 2025 m^2 area were collected by hand, and at the end of the 45-min search, were distributed evenly outside the area i.e., 20 – 25 m away from the plots. In total, 11 different divers participated with *C. schmideliana* removal/relocation during the course of the experiment. All divers were trained with the search protocol and experimental design before commencing the method. As described, *C. schmideliana* individuals were not culled during this experiment but merely relocated outside experimental perimeters to recreate the effect of complete removal in test treatment plots. Hence, it is highly possible individual *C. schmideliana* could 're-enter' test treatment search areas between removal dives.

Monitoring *C. schmideliana* predation

Coral transplants and recruits predated by *C. schmideliana* were recognised and confirmed by their bright-white, exposed and undamaged (typical of 'browsing' corallivores) calcium carbonate skeleton (Islands et al. 1960; Rotjan and Lewis 2008). As *C. schmideliana* primarily predate on small colonies (< 10 cm) that they can fully digest, the majority of predation instances were of the whole colony. Predated corals were usually in close proximity to other corals of a similar condition in an obvious path, and also nearby (1 – 2 m) *C. schmideliana* individual(s) (Bruckner and Coward 2019). Additionally, *C. schmideliana* feeding scars are also evident by the homogenous progression of turfing algae on the skeleton post-predation. This is in contrast to more heterogenous algal patterns which can indicate coral predation by *Drupella* spp., or indeed corals suffering white syndrome or banding diseases (Miller et al. 2009). However, to ensure that the sign is not from a particularly rapid necrosis, regular and frequent monitoring was paramount. As such, data was collected once a week, but all sites and treatment plots were also visually assessed mid-week. Clusters of transplanted coral were inspected closely during monitoring and individual coral fragments were categorised as either alive or dead. Within each of these 'major' categories, we established sub-categories whereby they were recorded as alive with > 75% tissue cover; alive with < 75% tissue cover; alive with partial predation by *C. schmideliana* (some tissue predated); alive with partial *Drupella* spp. predation; alive with partial fish predation (uncategorized but included physical damage to coral from fishes); alive with signs of bleaching; alive with presence of disease (uncategorized but included all visible disease); dead with 100% tissue predation by *C. schmideliana*; dead (uncategorized but included all deaths not attributed to *C. schmideliana*); or loose (fragments that were dislodged by wave action, fish, or other means). Natural colonies within quadrats were recorded in the same way, without the loose sub-category. The total accumulated predation by *C. schmideliana* was observed weekly during the study. Photographs were taken at the beginning and end of the study period of all clusters and circular quadrats. Recorded data was standardised through only one field observer.

Post-monitoring (up to 27 weeks)

Due to logistical constraints and time availability, the first two sites ('OOTB R' and 'Watersports'), which were monitored from March – May, were not monitored further after the original nine-week period. The latter three sites ('OOTB L', 'OOTS L' and 'Nursery') monitored initially from June – August were, however, continued until December (for an additional 18 weeks). This was undertaken to observe longer-term trends in our coral transplant survivorship. After the initial nine-week study, we stopped removing *C. schmideliana* across the plots. The sites were then monitored three times at six-week intervals, up to the 27-week mark. At each subsequent six-week interval, the status of coral transplants within clusters at both control and test treatments were recorded in a more nuanced categorisation to that outlined above, i.e., separated as alive with > 75% tissue cover; alive with < 75% tissue cover; dead with 100% tissue predation by *C. schmideliana*; dead (uncategorized but included all deaths not attributed to *Culcita*); or loose (fragments that were dislodged by wave action and/or fish). The total accumulated number of transplants predated on by *C. schmideliana* was also calculated at each six-week interval during post-monitoring. Due to the infrequency of post-monitoring, *C. schmideliana* predation was only confirmed if corals met the conditions highlighted above.

Data analysis

We carried out all statistical analysis and graphical representations using RStudio (Version 2021.09.2) with the packages tidyverse (Wickham et al. 2019), ggpubr (Kassambara 2020), and rstatix (Kassambara 2021). To test for significant differences in *C. schmideliana* densities at different sites we checked for normal distribution of the data using the Shapiro Wilk test and conducted Levene's test for homogeneity of variances. Both tests failed, hence we conducted a Kruskal–Wallis test followed by post-hoc analysis using Dunn's test for non-parametric data with pairwise comparisons and Bonferroni adjustment. To test for the effects of treatment over time for both recruits and transplants, we employed linear mixed-effects models. The models were fitted using the Restricted Maximum Likelihood (REML) estimation method using the "mixed()" function from the afex package (Singmann et al. 2012), with "Treatment" and "Week" as fixed effects, and "Site" as random term in each model, to account for pseudo-replication due to repeated sampling of the same reefs over time. To assess the significance of fixed effects, t-tests were performed, and Satterthwaite's method was employed for the calculation of degrees of freedom. In our analysis, degrees of freedom were determined using the Kenward-Roger method. This method is preferred in mixed-effects models as it provides more accurate estimates, especially in scenarios with small sample sizes or complex variance–covariance structures (Luke 2017). Post-hoc analysis was done using the "emmeans()" function from the emmeans package (Searle et al. 2012), to obtain estimated marginal means for each combination of "Treatment" and "Week", followed by pairwise comparisons, applying Tukey's adjustment to control for multiple comparisons, to assess differences between "Treatment" within each "Week". We also ran a simplified version of the generalized linear model for the final week of monitoring *C. schmideliana* predation with the aim of illustrating treatment effect specifically. We considered results to be significant with a p-value lower than 0.05 ($p < 0.05$) and displayed them as mean ± standard error. The R script used to create the figures and conduct the statistical analyses can be found on GitHub (https://github.com/SelmaMezger/ProjectCulcita).

Results

Population surveys

Average *Culcita schmideliana* density (as a mean across all sites) was recorded as 2.0 individuals per 100 m^2. The site with the highest density was 'Watersports'—with a density of 3.3 per 100 m^2, followed by 'Nursery' (2.3 per 100 m^2); 'OOTB L' (1.7 per 100 m^2); 'OOTB R' (1.3 per 100 m^2); and 'OOTS L' with the lowest density (1.2 per 100 m^2) (Fig. 3). The maximum number of *C. schmideliana* recorded on one transect was 14 (7.0 per 100 m^2) at 'Watersports' and the minimum was zero individuals at 'OOTS L' on two occasions. Statistical analysis revealed a significantly higher *C. schmideliana* density at 'Watersports' compared to 'OOTB R' (p = 0.014) and 'OOTS L' (p = 0.009) with a large effect size (eta2[H] = 0.22). No *Acanthaster* were observed on any of the surveys.

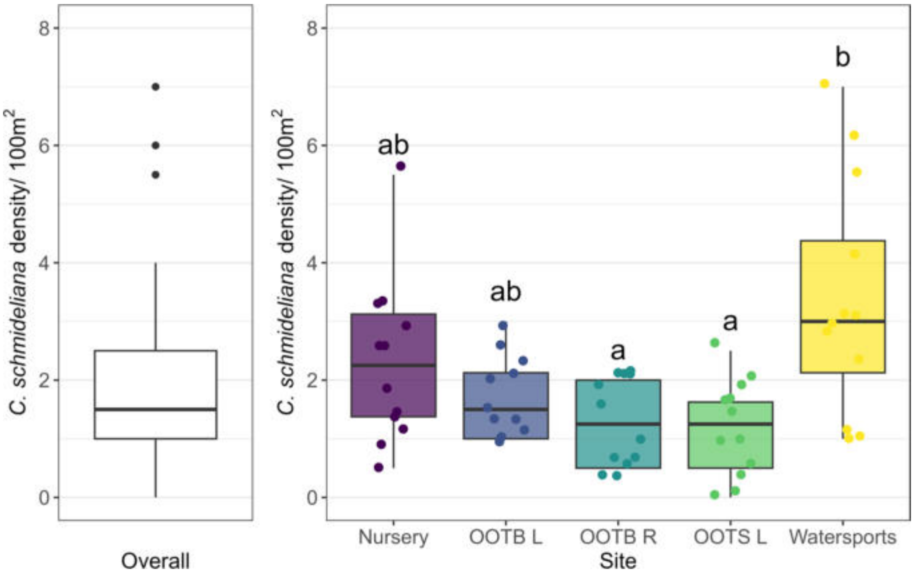

Fig. 3 Densities of *Culcita schmideliana* across all transects (overall) and by site. Each site was randomly surveyed during the study period (November 2022 – November 2023, n = 12 times). The median of each site is represented by the black horizontal line and each separate measurement is indicated by a dot in the respective colour of the site. Letters above plots indicate significant differences between sites ($p < 0.05$)

Observations within control treatment plots (*C. schmideliana* not removed)

The average predation rate across all five control plots was 24.6% for transplanted coral and 9.5% for recruits after nine weeks (Fig. 4). The highest level of predation (43.0% of transplanted coral; 7.3% of recruits) was recorded at ‘Watersports’ and the lowest at ‘OOTB L’ (11.0% of transplanted coral; 3.6% of recruits) and ‘OOTS L’ (11.0% of transplanted coral; 3.8% of recruits). ‘OOTB R’ was the second least densely populated site (Fig. 3) but recorded the second highest level of *C. schmideliana* predation (34.0% of transplanted coral; 9.7% of recruits). Overall, a greater number of transplanted coral (n = 123) were predated on than recruits (n = 44) in control plots (Table 1). There was also no significant effect of coral genus on predation (Table 2), hence data for both *Acropora* and *Pocillopora* was grouped together for all further statistical analysis. Within the nine-week study, 92.8% of predation cases (transplants and recruits) were fully digested, with only 12 cases of partial predation recorded, which were not included in the total predation results above.

A Mixed Model ANOVA revealed highly significant differences in *C. schmideliana* predation on coral type (‘recruit’

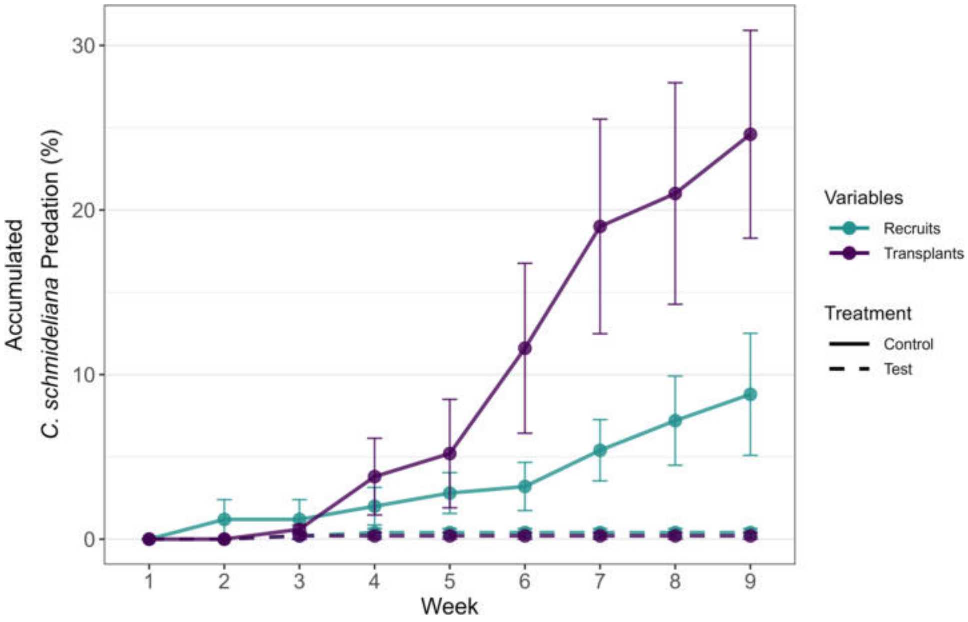

Fig. 4 Average predation (% of total) of recruits (n = 465 in control; n = 508 in test) and transplants (n = 500 in control and test) by *Culcita schmideliana* over nine weeks. Dots show the mean, with error bars displaying the standard error (n = 5 sites)

Table 1 Total values of coral transplants and recruits at the beginning of the study (t0) and at the end of regular monitoring (nine weeks). Total number of dead coral fragments/colonies equates to all recorded mortalities, including *Culcita schmideliana* predation

Transplants						Recruits			
		n(tQ)	Number of fragments predated by *C. schmidehana*	Total number of dead fragments	n (9 weeks)	n(tO)	Number of colonies predated by *C. schmidehana*	Total number of dead colonies	n (9 weeks)
Control	OOTB R	100	34	36	64	124	12	13	117
	Watersports	100	43	60	40	41	3	3	36
	OOTB L	100	11	12	88	110	4	4	84
	OOTSL	100	11	16	84	78	3	3	70
	Nursery	100	24	27	73	112	22	22	70
	Total	500	123	151	349	465	44	45	377
Test	OOTB R	100	0	4	96	148	0	0	148
	Watersports	100	1	22	78	30	0	3	23
	OOTB L	100	1	2	98	97	1	2	83
	OOTSL	100	0	1	99	92	0	0	86
	Nursery	100	0	1	99	141	1	1	132
	Total	100	2	30	470	508	2	6	472

Table 2 Total values of *Acropora* and *Pocillopora* corals (recruits and transplants) predated by *Culcita schmideliana* after nine weeks in control treatment plots (n = 5)

	Transplants			Recruits		
	n(tO)	Number of fragments predated by *C, schmideliana*	% of total	n(tO)	Number of colonies predated by *C. schmidehana*	% of total
Acropora	250	67	26.8	183	15	8.2
Pocillopora	250	56	22.4	282	29	10.3
Total	500	123	24.6	465	44	9.5

or 'transplant') ($p < 0.001$), time ($p < 0.001$), and their interaction ($p = 0.014$). The subsequent pairwise comparisons revealed significant differences in predation on recruits versus transplants starting from Week 7 onwards (Weeks 7 and 8: $p = 0.002$; Week 9; $p < 0.001$) (Fig. 4).

Within the five control plots, there was an overall mortality (inclusive of *C. schmideliana* predation) of 30.2% transplants (n = 151) and 9.7% recruits (n = 45) (Table 1). Other causes of mortality were identified as coral bleaching, competing algae, and other minor corallivory (*Drupella* spp. and fishes). Six fragments (1.2%) became loose in control sites and were no longer monitored. Predation by *C. schmideliana* constituted most of the mortality (85.2%) observed on recruits and transplants. A total of 96.7% of surviving transplants and recruits in control treatments were considered 'healthy' (> 75% alive tissue) after nine weeks.

Observations within test treatment plots (*C. schmideliana* removed)

A total of 412 *C. schmideliana* individuals were removed from test treatment plots throughout the nine-week study. The removal effects resulted in only four corals being predated in test plots: two transplanted fragments (0.4% of total) and two recruits (0.4% of total) (Table 1). Predation in test plots on transplants and recruits decreased on average by 24.2% and 9.1% respectively when compared to the control plots.

The Mixed Model ANOVA revealed highly significant differences in *C. schmideliana* predation on both recruits and transplants for treatment (recruits: $p < 0.001$; transplants: $p < 0.001$), time (recruits: $p < 0.001$; transplants: $p < 0.001$) and their interactions (recruits: $p < 0.003$; transplants: $p < 0.001$) (Supplementary Table S1-2), with the control treatment consistently exhibiting higher predation rates than the test treatment (Fig. 4). Post-hoc analysis with pairwise comparisons revealed that the differences in predation between both treatments started to be significantly different from Week 7 onwards for recruits (Week 7: $p = 0.002$; Weeks 8 and 9; $p < 0.001$), and Week 6 onwards for transplants (Week 6: $p = 0.005$; Weeks 7, 8 and 9: $p = 0.001$) (Supplementary Table S3-6).

Additionally, we analyzed the effect of the treatments in the final week on transplant and recruit predation rates using a generalized linear model (GLM, see Supplementary Table S7-10). The predicted transplant predation rate for the control treatment was 24.6 (SE = 2.22). In contrast, the predicted rate for the test treatment was significantly lower at 0.2 (SE = 0.20). For recruits, the predicted predation rate in the control treatment was 8.8 (SE = 1.327), and in the test treatment was also significantly lower at 0.4 (SE = 0.283). Pairwise comparisons between the control and test groups revealed a significant difference in transplant and recruit predation rates ($p < 0.0001$ for both), indicating that all coral in the control treatments experienced substantially higher predation rates compared to the coral in the test treatments.

Total mortality at the five test plots was low, with 5.8% of transplants (n = 29) and 1.2% of recruits (n = 6) dead after nine weeks (24.2% and 8.8% lower than control treatments, respectively). Similar to the control plots, mortality was attributed mainly to coral bleaching, diseases and competing algae. Seven fragments (1.4%) became loose during the study and were no longer included in the study. A total of 98.2% of surviving transplants and recruits in test treatments were considered 'healthy' (> 75% alive tissue) after nine weeks.

Post-monitoring of transplants at three sites

Predation of transplanted coral at control treatments remained higher than test treatments after 27 weeks, with a total number of predated corals at 96 (32.0%) and 77 (25.7%) respectively (Table 3). A 25.4% rise in overall predation was observed from week 9 to 27 following the recontinued presence of *C. schmideliana* (Fig. 5). The 'Nursery' site exhibited the highest levels of confirmed predation across the three sites, in both control (62.0%) and test (52.0%) treatment plots after 27 weeks (Table 3). Prior to the cessation of *C. schmideliana* removal (week 9), the 'Nursery' test treatment plot observed zero confirmed predations.

The overall mortality of corals across test treatments rose from 4 fragments (1.3%) in week 9 (Table 1), to 121 fragments (40.3%) in week 27 (Table 3). Mortality across control treatments also continued to increase from 55 fragments (18.3%) in week 9, to 176 fragments (58.7%) in week 27. Confirmed predation by *C. schmideliana* constituted the majority of this recorded mortality (58.0%) across all sites and treatments, with other causes of mortality (37.0%) attributed to various

Table 3 Total values of coral transplants at the beginning of the study (t0) and at the end of post-monitoring (27 weeks). Total number of dead coral fragments is all mortalities recorded, including *Culcita schmideliana* predation

		Transplants			
		n(tO)	Number of fragments predated by *C, schmideliana*	Total number of dead fragments	n(27 weeks)
Control	OOTB L	100	17	36	64
	OOTSL	100	17	48	52
	Nursery	100	62	92	8
	Total	300	96	176	124
Test	OOTB L	100	24	38	62
	OOTSL	100	1	18	82
	Nursery	100	52	65	35
	Total	300	77	121	179

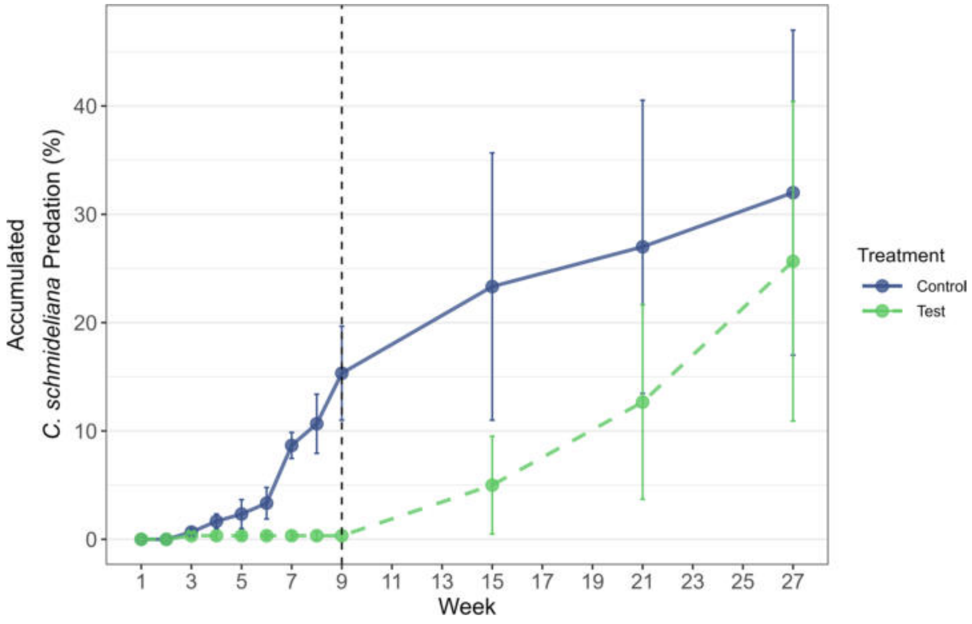

Fig. 5 Average *Culcita schmideliana* predation (% of total) of transplanted coral (n = 300) at control and test treatments over 27 weeks. Removal of *C. schmideliana* ceased in test treatments after nine weeks (dashed back line). Dots show the mean, with error bars displaying the standard error (n = 3 sites)

coral diseases, competing algae, bleaching, other corallivory and unknown causes. We recorded 31.0% of this unknown mortality as being likely predated by *C. schmideliana*. Further, 5.0% of corals became loose during the 27-week study and were not monitored. Mortality at the ‘Nursery’ was the highest of the three sites in both the control and test treatments (92.0% and 65.0% respectively). A total of 84.2% of surviving transplants in all treatments and sites were considered ‘healthy’ (> 75% alive tissue) after 27 weeks.

Our analysis revealed significant effects of *C. schmideliana* predation dynamics on coral transplants, considering both the treatment ($p = 0.006$) and time ($p = 0.021$). Interestingly, the interaction effects between treatment and time periods were not statistically significant ($p = 0.779$), indicating that the slopes of predation over time did not significantly differ between the control and test treatments following the cessation of *C. schmideliana* removal (week nine) (Fig. 5). The estimated intercept for the control site was 15.33, although again this was not statistically significant ($p = 0.226$). This may be indicative of a prior elevated baseline level of predation in the control treatment during the initial period of the study, especially when compared to the previously ‘protected’ test treatment sites.

The random effects analysis indicated variability between sites in the intercept, with a larger variance for the intercept (site: variance = 230.3, standard deviation (SD) = 15.18) compared to the residual variance (residual: variance = 106.1, SD = 10.30). The variability in intercepts across sites emphasizes the importance of considering site-specific factors in *C. schmideliana* predation dynamics.

Discussion

Population densities and associated predation rates

Here we show predation rates of *Culcita schmideliana* on both transplanted corals and natural recruits around

Kunfunadhoo Island in the Maldivian archipelago. Of the 465 monitored natural recruits (across the five control treatment plots), average mortality from *C. schmideliana* predation was 9.5% after a nine-week period (n = 44). This is lower than other observations found within the Maldives; For example, Bruckner and Coward (2019) reported *C. schmideliana* recruit predation of up to 24.0% in a single observation in Raa Atoll. However, this difference in predation rate is most likely due to the higher observed densities found in that location compared to ours (7.0 ± 1.4 individuals per 100 m^2 vs. 1.2 – 3.3 per 100 m^2 respectively). The level of predation observed on Kunfunadhoo did, however, have a substantially negative effect on the survival of recruits and transplanted corals. We showed average *C. schmideliana* predation levels on transplanted corals of 24.6%, with 'Watersports' recording 43.0% transplant predation after only a nine-week period. Although some corals in this study were likely to grow past the predation size threshold of *C. schmideliana*, it may be safe to assume that mortality could approach close to 100% within a year. Interestingly, although population densities around Kunfunadhoo are relatively low (compared to others reported in the Maldives), they are still considered high when compared to studies conducted in other locations. For example, in Saipan and French Polynesia, levels of less than 0.5 individuals of *C. novaeguineae* were reported per 100 m^2 (Quinn and Kojis 2003; Pratchett et al. 2011). Further, if we compare the mean densities recorded in our study to other corallivorous asteroids, we may even declare these as 'outbreak' levels, considering *Acanthaster* populations exceeding 0.2 – 0.4 individuals per 100 m^2 are classified in this respect (Pratchett 2005; Bruckner et al. 2019; Montalbetti et al. 2018). However, we are not at a stage where we can ascertain what a normal population level of *C. schmideliana* is on any given reef, at least until a wider survey across multiple sites is undertaken. Long-term surveys are also needed to account for any periodic population fluctuations described for some echinoderms such as *Acanthaster* spp., in response to changing ecosystem structure (Uthicke et al. 2009; Pratchett et al. 2017). Future studies may wish to effectively time the removal of *C. schmideliana* in response to such cyclical patterns of increased densities. Such a practice may potentially reduce mitigation effort in seasons with lower sea-star densities. Further, in order to truly characterise what may be considered as an 'outbreak' density of *C. schmideliana*, we must first understand a coral reef's threshold to withstand certain levels of background predation—given that background mortality is a normal component of natural systems, important to ensure diversity, survivability and reef function (Hughes and Jackson 1985; Bythell et al. 1993; Pisapia and Pratchett 2014). Regardless of whether or not we have hit plague proportions, what we can confirm is that the population densities recorded here are severely disadvantageous for effective reef recovery and transplantation at the survey sites.

Effect of coral genus and type on predation

Interestingly, we found no significant difference, and therefore preference of *C. schmideliana* predation across coral genera (*Pocillopora* spp. and *Acropora* spp.). This is in contrast to others who have historically reported a preference for *Pocillopora* spp. (Bruckner and Coward 2019; Montalbetti et al. 2018). One explanation for these variable results may be the relative abundance of the prey (typically equal amounts across genera), which has impacted the predator–prey dynamics of *C. schmideliana* in this study, perhaps making them more generalist in nature. A significant difference in the predation rates between natural recruits and transplanted corals was, however, detected. Transplanted corals were more frequently predated than natural recruits within the same survey area. This may be explained by the size and distribution of the individual corals monitored. Natural recruits represented a wider spread of sizes (in theory, any noticeable size between settlement and 10 cm colony). A portion of these monitored recruits may very well lie outside of the dietary preferences of *Culcita* spp., which Glynn and Krupp (1986) suggest is between 3 and 8 cm. Our personal field observations report that small recruits (< 2 cm) were very rarely predated on. In contrast, the size of our transplants (consistently around ~ 7 cm), certainly appears to reflect the preferential/optimum size of coral that *C. schmideliana* target (Montalbetti et al. 2018; Bruckner and Coward 2019). In addition, transplants in our study were only cemented onto flat surfaces for ease of fixing and adhesion. It is hypothesized that the anatomy of *Culcita* spp., i.e., their round body and lack of prehensile arms, hamper their ability to climb complex three-dimensional structures (Thomassin 1976; Montalbetti et al. 2022). Therefore, it is likely that foraging on the low-lying transplant clusters was more common due to ease of access when compared to the topography within the recruit quadrats, which were made up of vertical surfaces, crevices and coral heads (Raj et al. 2018). Furthermore, transplants were also cemented near each other (10 fragments within a ~ 0.25 m^2 area), meaning that a random encounter of one transplant by a *C. schmideliana* would likely result in more transplants being encountered during its search.

Effect of *C. schmideliana* removal on overall coral mortality

In contrast to the control treatments, minimal predation (0.4% of transplants and recruits) was observed in test treatments that underwent routine predator removal, as well as marked reductions in overall mortality, owing to decreased *C. schmideliana* feeding. Removal of corallivorous predators as a passive tool for restoration is certainly not a new idea and has been well studied (Williams et al. 2014; Nakamura et al. 2016; Chak et al. 2018; Shaver et al. 2018). For example, Westcott et al. (2020) showed that manual *Acanthaster* removal increased hard coral cover by 17.6% after four and a half years. Interestingly, as we did not cull the cushion stars in our study (instead merely relocating them), we were unable to explore longer term impacts of removal at this site. However, such further studies are encouraged. Despite this lack of long-term data, our results do clearly show that a suppression of chronic *C. schmideliana* predation favours the survival of both transplanted and naturally recruited *Acropora* and *Pocillopora* at the local scale. This is an important measure to enable natural reef recovery, and in our case actively restore degraded areas effectively, especially in the aftermath of recent mass bleaching events (Pratchett et al. 2013; Pisapia and Pratchett 2014; Morri et al. 2015; Pisapia et al. 2015, 2019; Ibrahim et al. 2017). Interestingly, there is a strong argument that successful passive restoration can potentially dismiss the necessity for active restoration efforts (Westcott et al. 2020). However, in many cases it may not be sufficient to preserve biodiversity and associated ecological functions during global reef decline, making active restoration increasingly more essential to assist reef management (Edwards and Gomez 2007; Rinkevich 2014; Boström-Einarsson et al. 2020; Madin et al. 2023). As Possingham (2015) describes, successful conservation outcomes can be better achieved, where possible, by combining both restoration (active) and protection (passive) approaches. It appears that *C. schmideliana* removal operates on both of these fronts, by effectively safeguarding transplanted coral, and by limiting chronic background mortality on natural recruits.

Post-monitoring of transplants and recolonisation of *C. schmideliana*

The cessation of the *C. schmideliana* removal following the initial nine-week study also revealed the ineffectiveness of relocating rather than culling. The high numbers of surviving transplants in test treatment plots were in danger instantaneously once *C. schmideliana* removal stopped. In one of our sites (‘Nursery’), 99 surviving transplants in the test plot dropped to 35 in the ensuing 18 weeks after *C. schmideliana* recolonisation, with most mortality (at least 84.0%) owing to confirmed *C. schmideliana* predation. In order to have maintained the survival of these fragments, it appears continued labour-intensive relocation of *C. schmideliana* would have had to occur in the same manner as described in our methodology. A culling regime involving complete removal of these coral predators would certainly remove the pressure of returning *C. schmideliana* observed in our post-monitoring study, and limit continued intervention.

Implications for coral restoration

Our study presents three interesting tools that reef practitioners can utilise. First, there is strong support and justification for the harbouring of coral within protected *ex-situ* or *in-situ* nurseries for longer periods before transplantation. This is (in this instance), for them to grow past preferred predation size thresholds of *C. schmideliana* before transplantation. Although we recognise there are additional costs to such practices, the benefits of reduced grazing/predation and ultimately increased survivorship has been shown to have a positive benefit–cost ratio elsewhere (Humanes et al. 2021). Secondly, dispersing fragments among more complex, rugose transplantation sites can perhaps ‘hide’ coral fragments from foraging *C. schmideliana* that struggle to navigate such terrain. Although we did not directly investigate these two practices, combined they are almost certainly going to improve transplanted coral survivorship. The third of course involves the passive removal of *C. schmideliana* akin to that of *Acanthaster* management (Westcott et al. 2020). Interestingly, this is the first study to suggest population management of *C. schmideliana* as we show it to be an effective and viable technique for significantly increasing transplanted coral survival, as well as reducing background mortality on coral recruits. A sensible strategy for effective restoration going forward may be to combine all three techniques.

Conclusion

Our findings reveal key insights into the background corallivorous effects of *C. schmideliana* over time, in both natural and coral restoration settings. Our work clearly reinforces previous studies that highlight *C. schmideliana* as a concerning predator on young coral recruits and, now additionally, coral transplants. We provide a basis for subsequent monitoring of the efficacy of *C. schmideliana* removal, and its potential long-term positive and negative effects on the recovery of coral reefs. Such a management strategy may be the assisted step needed to enable certain reefs in the Indo-Pacific to recover between major stress events, through the increased survivability of transplanted coral and the successful recolonisation of coral recruits.

Acknowledgements This research took place at Soneva Fushi Resort. We would like to acknowledge and thank Soneva and Soneva Foundation for their continued support throughout this research, as well as the entire 2022 – 2023 Soneva Fushi Science and Conservation team for their contributions towards data collection. Matthew Walker extends additional gratitude to Zoe Tapps for her invaluable assistance and patience shown in the process of producing this manuscript.

Author contributions Conceptualisation: Matthew Walker; Methodology: Matthew Walker; Data collection: Matthew Walker, Aiden Clarke; Data Curation: Matthew Walker; Formal analysis: Selma Mezger, Matthew Walker; Investigation: Matthew Walker, Aiden Clarke; Project administration: Matthew Walker; Writing—original draft preparation: Matthew Walker, Michael Sweet; Writing—review and editing: Matthew Walker; Michael Sweet, Jamie Craggs, Selma Mezger, Igor Pessoa, Johanna Leonhardt; Funding acquisition: Ahmad Allahgholi; Resources: Ahmad Allahgholi, Johanna Leonhardt; Supervision throughout the project: Michael Sweet, Jamie Craggs. All authors have read and agreed to the published version of the manuscript.

Funding Soneva Foundation

Declarations

Conflict of interest Matthew Walker, Aiden Clarke, Igor Pessoa, Johanna Leonhardt and Ahmad Allahgholi were employed by Soneva Fushi Resort during this study. This study was funded by Soneva Foundation. The other authors received no funding for their contributions and report no conflicts of interest.

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