Understanding the species richness of cleaning stations and ecological role of cleaning symbioses in Laamu Atoll, Maldives, using data from Remote Underwater Video (RUV) surveys

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Abstract

Coral reefs are highly productive marine ecosystems that support a range of biological processes, including cleaning symbioses. To date, previous studies have focused primarily on reef manta rays (*Mobula alfredi*) and there is a lack of research concerning cleaning interactions of other megafauna. This study aims to examine the effects of cleaning station, habitat complexity, and moon phase on species richness, relative abundance (MaxN) of megafauna, and cleaning interaction duration of megafauna across six cleaning stations in Laamu Atoll, Maldives. Remote Underwater Video (RUV) surveys (*n* = 39) were conducted across cleaning stations from September 2022 to April 2023. A total of 153 species from 33 families and 14 orders were identified across cleaning stations. Generalised Linear Models (GLMs) were used to show that habitat complexity had a statistically significant effect on species richness, with cleaning stations with a habitat complexity score of 4 having the greatest mean number of species (75.00 ± 2.83). Cleaning station, habitat complexity, and moon phase had statistically significant effects on cleaning interaction duration of megafauna. Yellow Block cleaning station (16.80 ± 20.70), habitat complexity score of 3 (21.80 ± 27.20), and the New Moon phase (19.30 ± 24.20) showed longer mean cleaning interaction durations. These findings highlight how important structurally complex coral reefs are for supporting cleaning symbioses and suggest that conservation efforts should be targeted towards protecting these sites and the megafauna that utilise them. Furthermore, anthropogenic pressures are expected to increase habitat degradation and future research would benefit from regular monitoring of these cleaning stations and a deeper understanding of the dynamics of cleaning symbioses and costs of these mutualistic interactions at a species and population level.

Introduction

Cleaning Symbioses

Monitoring sites where ecologically important activities take place is crucial for informing effective conservation and management (Barr and Abelson, 2019; Perryman *et al.,* 2019). The marine environment is particularly vulnerable to climate change and regular monitoring is crucial for maintaining the integrity of these ecosystems and advancing our understanding of complex biological processes, such as cleaning symbioses (Giddens *et al*., 2022). Cleaning symbioses are widely documented throughout scientific literature and have been studied across a range of taxa and environments (Côté and Mills, 2020; Caves, 2021). However, the majority of research in this field has focused on the marine environment and the mutualistic relationship between cleaner and client organisms (Vaughan *et al.,* 2017; Caves, 2021). For the purpose of this study, cleaning symbiosis will be defined as *"the removal of ectoparasites, bacteria, diseased and injured tissue, and unwanted food particles by cleaner organisms from cooperative host organisms"* (Feder, 1996). Cleaning symbioses take place on cleaning stations, discrete areas of coral reef occupied by populations of cleaner species (Triki *et al.,* 2019). These microhabitats are typically characterised by scleractinian corals and provide resident species with increased cleaning opportunities and protection from predation (Whittey *et al*., 2021). Bluestreak cleaner wrasse (*Labroides dimidiatus*) are one of the most widely studied cleaner organisms on coral reefs (Araujo *et al.,* 2020; Demairé *et al.,* 2020; Knight, 2022). However, more than 208 fish species have been identified as cleaner organisms, highlighting the prevalence of cleaning symbioses in the marine environment (Narvaez *et al.,* 2021).

Previous research has focused primarily on environmental factors limiting the ecological benefits of cleaning symbioses. These include cleaning station substrate (Armstrong *et al*., 2021), wind direction (Harris *et al*., 2020), and moon phase (Couturier *et al*., 2018). Reef manta ray (*Mobula alfredi*) studies have dominated this field and several researchers have demonstrated the effects of moon phase on frequency of cleaning interactions (Barr and Abelson, 2019; Carpenter *et al*., 2023; Mallevoue, 2023). For example, Harris and Stevens (2021) reported increased visitation rates of reef manta rays (*Mobula alfredi*) during the New Moon and Full Moon phases, suggesting that moon phase is an important predictor of cleaning interaction frequency. This relationship has been studied across ocean basins and researchers believe that decreased illumination and foraging opportunities during these phases provides a potential explanation for increased frequency of cleaning interactions (Barr and Abelson, 2019; Harris and Stevens, 2021; Fonseca-Ponce *et al*., 2022). However, there is a significant lack of research concerning the effects of habitat complexity on cleaning symbioses and further research is required to determine how important this factor is in determining the quality of cleaning interactions in the marine environment.

Applications of underwater camera technology

Applications of underwater camera technology have grown in recent years due to improvements in battery power and data processing (Bicknell *et al*., 2016; Bergshoeff *et al*., 2017). These technologies provide an alternative data collection method for sampling remote locations and can be deployed in challenging environmental conditions (Erickson, Bugnot and Figueira, 2023). In particular, they have enabled researchers to gain insight into the biodiversity of marine ecosystems and ecological role of cleaning symbioses (Schofield *et al*., 2017). Baited Remote Underwater Video (BRUV) surveys are commonly used to assess community structure and the population dynamics of target species (Devine, Wheeland and Fisher, 2018; Sherman *et al*., 2018; Espinoza *et al.,* 2020). However, this method of Underwater Visual Census (UVC) can disrupt natural foraging behaviours and attract a disproportionate number of carnivorous species (Caldwell *et al*., 2016; Logan *et al*., 2017; Rhodes *et al*., 2020). Applications of this technology have decreased in recent years, due to the limited understanding of bait plume effects (Jones *et al*., 2020; Coro and Bjerregaard Walsh, 2021; Erickson, Bugnot and Figueira, 2023). Remote Underwater Video (RUV) surveys provide an alternative method for monitoring ecosystem health and cleaning symbioses in the marine environment (Piggott *et al*., 2020). This technology is suitable for behavioural studies, as it is less invasive and produces more robust research findings (Rhodes *et al*., 2020). However, increased sampling effort is required to collect the same volume of data due to decreased field of view (FOV) saturation (Erickson, Bugnot and Figueira, 2023).

The Maldives

The Republic of Maldives is an independent state located in the Indian Ocean (Hudgins *et al*., 2023). This archipelago stretches 860km and comprises 1,192 islands with a total land surface area of 298km^2 (Hilmi *et al.,* 2023). The Maldives is known for its rich biodiversity and productive marine ecosystems (Stevens and Froman, 2019). 258 scleractinian coral species belonging to 57 genera and over 1,200 fish species have been identified (Stevens and Froman, 2019; Abdulla and Techera, 2021). However, there is a lack of knowledge regarding the distribution and relative abundance of these species, which is particularly concerning for the 52% of elasmobranchs listed as threatened by the International Union for Conservation of Nature (IUCN) (Stevens and Froman, 2019). Furthermore, the Maldives is threatened by a host of anthropogenic pressures, including destructive fishing practices, unsustainable tourism and climate change (Sharma and Sommer, 2022; Strike *et al*., 2022). Coral bleaching is one of the most widely recognised effects of climate change and several researchers have studied the ecological and socioeconomic impacts of this threat (Olguín-López *et al*., 2018; Ainsworth *et al*., 2021; Smith *et al*., 2021). For example, Cowburn *et al*. (2019) conducted a study investigating the 2016 mass bleaching event in North Ari Atoll, Maldives. In this study, researchers reported increased habitat degradation and population size of crown of thorns starfish (COTs) (*Acanthaster planci*) following the bleaching event (Cowburn *et al*., 2019). These findings are particularly concerning, as researchers believe that the structural complexity of coral reefs is positively associated with species richness and hence the quality of cleaning symbioses (Denis *et al.,* 2017; Whittey *et al*., 2021).

The majority of research investigating cleaning symbioses in the Maldives has been conducted on reef manta rays (*Mobula alfredi*) as they tend to frequent the same cleaning stations year-round (Harris and Stevens, 2021; Nicholson-Jack *et al*., 2021). In recent years, there has been an observed decline in reef manta ray (*Mobula alfredi*) abundance at Hithadhoo Corner, a popular dive site located in Laamu Atoll (Maldives Manta Conservation Programme, 2021). The Manta Trust requires a greater understanding of the species present and types of interactions occurring across cleaning stations in order to understand what makes them well functioning. This study aims to examine the effects of cleaning station, habitat complexity, and moon phase on (a) species richness, (b) relative abundance (MaxN) of megafauna, and (c) observed cleaning interaction duration of megafauna across six cleaning stations in Laamu Atoll, Maldives. These data will be used by the Manta Trust to develop a baseline understanding of the current state of cleaning stations in Laamu Atoll. They will also be used to create recommendations to be put forward on how best to monitor and evaluate these crucial sites.

Materials and Methods

Study Area

Laamu Atoll (N 1° 55’ 59.99” E 73° 24’ 59.99”) is the second largest atoll in the Maldives, located in the central south of the archipelago (Figure 1) (McNamara *et al*., 2019). It comprises 73 islands and has a population of approximately 12,000 (Clissold, McNamara, and Westoby, 2020). In this study, all spatial analyses were performed in QGIS (QGIS Development Team, 2023). Vector datasets in the World Geodetic System (WGS84) were sourced online and used for the analysis of this study. Spatial data was sourced from ‘DIVA-GIS’ (https://www.diva-gis.org/) and subnational administrative boundaries were sourced from ‘The Humanitarian Data Exchange’ (https://data.humdata.org/).

Data Collection

Thirty-nine Remote Underwater Video (RUV) surveys were conducted across six different cleaning stations in Laamu Atoll, Maldives, from September 2022 to April 2023 (Figure 1). These devices comprised one GoPro Hero 4 camera connected to an external battery pack or one GoPro Hero 8 camera, both set to film with a video resolution of 1080p. The RUVs were secured to cleaning stations by employees of the Maldives Manta Conservation Programme during routine scuba diving surveys. Deployment duration ranged from 27 minutes to 5 hours 43 minutes. A total of 66 hours 38 minutes of footage was captured from the deployments. Additional Moon phase data was sourced online and recorded for each deployment (Time and Date, N.D).

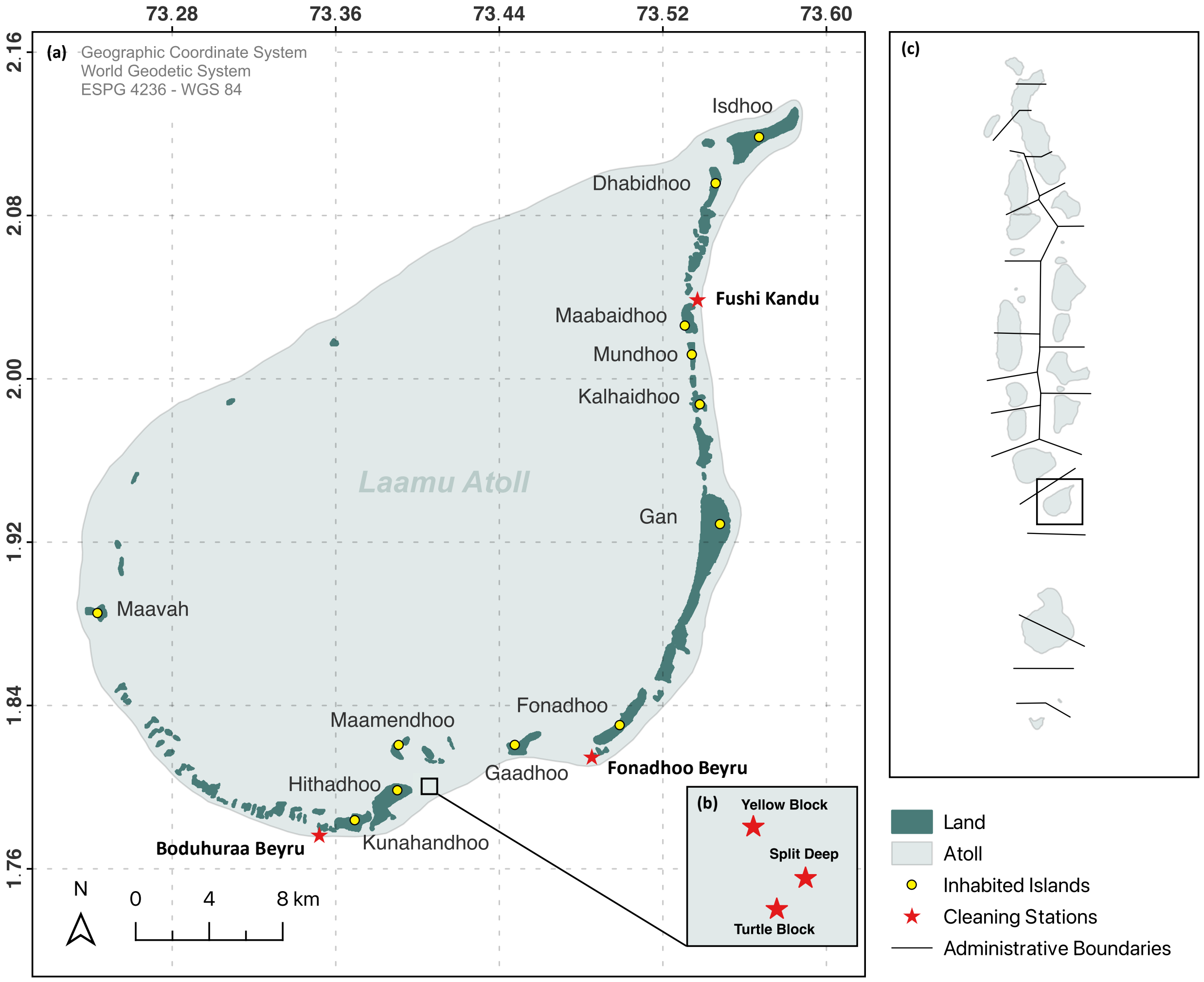

Figure 1. (a) Map of Laamu Atoll and location of cleaning stations (*n* = 6) where Remote Underwater Video (RUV) surveys were conducted (*n* = 39). Light blue polygon shows extent of the Atoll, inhabited islands are marked with a yellow point and cleaning stations are marked with a red star. **(b)** Inset map showing location of Hithadhoo Corner and Yellow Block, Split Deep, and Turtle Block cleaning stations. **(c)** Location of Laamu Atoll in the central south of the Maldivian archipelago. Administrative boundaries are marked by black lines.

Data Processing

RUV deployments were analysed independently by one observer. Deployments where the cleaning station was not visible in the FOV (*n* = 9) were excluded from further analysis to decrease sampling bias. The Visual Rugosity Index (VRI), as proposed by Polunin and Roberts (1993), was used to quantitatively estimate the habitat complexity of each deployment (Supplementary Materials; Table S1). Habitat classification was consistently performed 3 minutes into each deployment to allow for repositioning of the devices on the cleaning stations. The following VRI scale of 0 to 5 was used to classify habitat complexity *"0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous caves and fissures, 5 = exceptionally complex with high coral cover and numerous caves and overhangs"* (Polunin and Roberts, 1993).

The following variables were recorded per deployment:

(a) Species richness – defined as the number of species identified per deployment. The taxonomic species, family and order ranks were also recorded.

(b) Relative abundance (MaxN) of megafauna – defined as *"the maximum number of individuals observed of a species in a single frame"* (Sherman *et al*., 2018). The entry time of individuals and the taxonomic species, family and order ranks were also recorded. Megafauna belonging to the Chondrichthyes and Reptilia classes were the primary focus of this study.

(c) Observed cleaning interaction duration of megafauna – the whole duration of cleaning interactions could not be calculated, as client species entered and exited the FOV with cleaner organisms attached. Instead, observed cleaning interaction duration was recorded and defined as the amount of time (seconds) a cleaning interaction was observed in the FOV. Characteristic client behaviours were used to identify cleaning interactions, such as opening of the operculum and repositioning of the fins (Caves, Green and Johnson, 2018). Cleaner pecking behaviour was also used to identify cleaning interactions (Whittaker, Maeda and Boulding, 2021).

Data Analysis

All statistical analyses were performed in R with an alpha (α) significance level of 0.05 (V 4.2.2; R Core Team, 2022). Generalised Linear Models (GLMs) were used to examine the effects of cleaning station, habitat complexity, and moon phase on (a) species richness, (b) relative abundance (MaxN) of megafauna, and (c) observed cleaning interaction duration of megafauna. A Quasipoisson distribution was used to examine (a) species richness due to evidence of overdispersion. A Poisson distribution was used to examine (b) relative abundance (MaxN) of megafauna. A log transformation was applied and a Gaussian distribution was used to examine (c) observed cleaning interaction duration of megafauna. The `'drop1()'` function was used to obtain the significance of each predictor variable and compare all possible models by dropping a single term (V 4.2.2; R Core Team, 2022). Analysis of Variance (ANOVA) was then used to obtain a chi-squared (χ^2) statistic for reporting purposes. The `'glht()'` function and Tukey's Honest Significance Difference (HSD) tests were used to conduct post-hoc pairwise comparisons to test the levels within a significant categorical variable (V 1.4.25; Hothorn *et al*., 2008). The R `‘dplyr’` package was used to manipulate the data and perform statistical analyses (V 1.0.10; Wickham *et al*., 2022) and the R `‘ggplot2’` package was used to visualise the data and plot figures (V 3.4.0; Wickham, 2016).

Results

Thirty-nine Remote Underwater Video (RUV) surveys were conducted across six different cleaning stations in Laamu Atoll, Maldives. A total of 34 deployments were conducted at Hithadhoo Corner.

A further two deployments were conducted at Fushi Kandu and Boduhuraa Beyru and one deployment was conducted at Fonadhoo Beyru. Mean depth of cleaning stations sampled was 19.38 (± 4.55) metres and mean deployment length was 1 hour 51 minutes.

Species richness

A total of 153 species from 33 families and 14 orders were identified across the six cleaning stations in Laamu Atoll, Maldives (Supplementary Materials; Table S2). The most common species identified were the bluestreak cleaner wrasse (*Labroides dimidiatus*), bluefin jack (*Caranx melampygus*), eyeline surgeonfish (*Acanthurus nigricauda*) and orange basslet (*Pseudanthias squamipinnis*). Whilst 15 of the 153 species identified in this study were recorded at all six cleaning stations (Table 1), 32 of the species were recorded at only one cleaning station (Supplementary Materials; Table S3). There was no evidence of a statistically significant effect of cleaning station ($\chi^2_5 = 7.61$, $p = 0.60$; Figure 2a) on species richness. Yellow Block (70.70 ± 6.26; Figure 2a), Turtle Block (62.00 ± 10.60; Figure 2a) and Split Deep (59.30 ± 15.20; Figure 2a) cleaning stations, located in Hithadhoo Corner, had the greatest mean (± SD) species richness. There was a statistically significant relationship between habitat complexity ($\chi^2_4 = 56.25$, $p < 0.05$; Figure 2b) and species richness. Post-hoc testing revealed a statistically significant difference in species richness between habitat complexity scores 0 and 2 ($p < 0.05$). Cleaning stations assigned a habitat complexity score of 4 (75.00 ± 2.83; Figure 2b) had the greatest mean (± SD) species richness. Note that no cleaning station was assigned a habitat complexity score of 5 in this study. Lastly, there was no evidence of a statistically significant effect of moon phase ($\chi^2_3 = 32.52$, $p = 0.10$; Figure 2c) on species richness. The New Moon (67.90 ± 10.10; Figure 2c) and Third Quarter (63.40 ± 12.70; Figure 2c) phases had the greatest mean (± SD) species richness.

Table 1. Species identified at all six cleaning stations in Laamu Atoll, Maldives ($n = 15$).

Common Name	Scientific Name	Species Family	Species Order
Eye-line surgeonfish	*Acanthurus nigricaudus*	Acanthuridae	Acanthuriformes
Night surgeonfish	*Acanthurus thompsoni*	Acanthuridae	Acanthuriformes
Striped triggerfish	*Balistapus undulatus*	Balistidae	Tetradontiformes
Moon fusilier	*Caesio lunaris*	Caesionidae	Perciformes
Blue-fin jack	*Caranx melampygus*	Carangidae	Carangiformes
Double-bar puller	*Chromis opercularis*	Pomacentridae	Perciformes
Weber's puller	*Chromis weberi*	Pomacentridae	Perciformes
Fine-lined bristletooth	*Ctenochaetus striatus*	Acanthuridae	Perciformes
Blue-streak cleaner wrasse	*Labroides dimidiatus*	Labridae	Labriformes
Red bass	*Lutjanus bohar*	Lutjanidae	Perciformes
Sleek unicornfish	*Naso hexacanthus*	Acanthuridae	Acanthuriformes
Threadfin basslet	*Nemanthias carberryi*	Serranidae	Perciformes
Orange basslet	*Pseudanthias squamipinnis*	Serranidae	Perciformes
Ember parrotfish	*Scarus rubroviolaceus*	Scaridae	Labriformes
Moorish idol	*Zanclus cornutus*	Zanclidae	Acanthuriformes

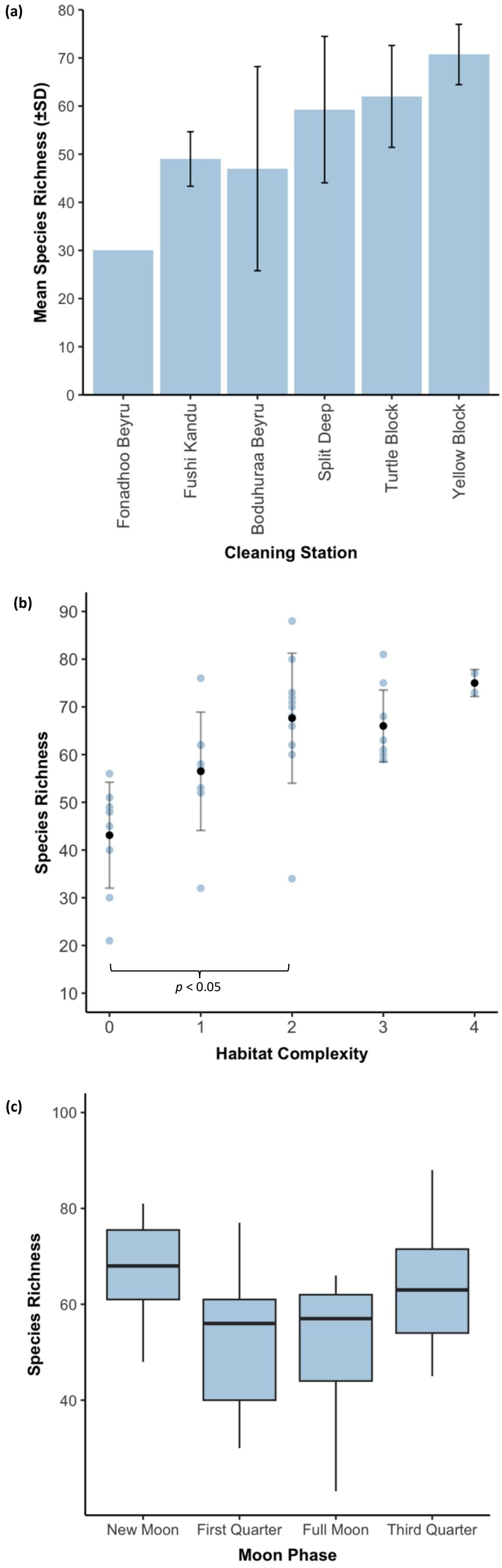

Figure 2. Examining the effects of cleaning station, habitat complexity, and moon phase on the species richness of cleaning stations across Laamu Atoll, Maldives. Statistically significant pairwise comparison is indicated by black bracket. **(a)** Mean species richness (± SD) of cleaning stations (*n* = 6) within all sampled deployment locations. Bars show mean species richness and are fitted with black standard deviation (± SD) error bars. Note that a ± SD could not be calculated for Fonadhoo Beyru, as one deployment was conducted at this location. **(b)** Species richness across cleaning station habitat complexities. Blue points show raw species richness data. Black points show mean species richness fitted with grey standard deviation (± SD) error bars. **(c)** Species richness across moon phases. Boxes denote interquartile range; horizontal black lines indicate median and whiskers extend from 25th to 75th percentiles.

Relative Abundance (MaxN) of Megafauna

A total of nine megafauna species from five families and three orders were identified across the six cleaning stations in Laamu Atoll, Maldives (Supplementary Materials; Table S4). The silvertip shark (*Carcharhinus albimarginatus*) (3.00 ± 0.00; Figure 3a), grey reef shark *(Carcharhinus amblyrhynchos)* (2.19 ± 1.56; Figure 3a) and whitespotted eagle ray (*Aetobatus oscellatus*) (1.75 ± 0.71; Figure 3a) had the greatest mean (± SD) relative abundance (MaxN) per deployment. A standard deviation (± SD) could not be calculated for the silvertip shark (*Carcharhinus albimarginatus*), as this species was recorded on only one deployment at Boduhuraa Beyru. Furthermore, the blotched fantail ray (*Taeniurops meyeni)* and blacktip reef shark *(Carcharhinus melanopterus)* had a ± SD of 0, as all values in the data set were the same. When calculating the mean relative abundance of megafauna per deployment, the total number of each species was divided by the number of deployments it was present in. This method takes into account variation across deployments and provides a more representative measure of abundance. There was no evidence of a statistically significant effect of cleaning station ($\chi^2_5 = 7.50$, $p = 0.19$) on MaxN of megafauna. Yellow Block cleaning station, located in Hithadhoo Corner, had the greatest mean (± SD) MaxN of grey reef shark (*Carcharhinus amblyrhynchos*) (3.86 ± 2.12). Whereas, Fushi Kandu cleaning station had the greatest mean (± SD) MaxN of whitetip reef shark (*Triaenodon obesus*) (2.50 ± 2.12). There was also no evidence of a statistically significant effect of habitat complexity ($\chi^2_1 = 0.04$, $p = 0.70$; Figure 3b) or moon phase ($\chi^2_3 = 4.18$, $p = 0.79$; Figure 3c) on MaxN of megafauna. Cleaning stations assigned a habitat complexity score of 3 (3.55 ± 1.29; Figure 3b) and the First Quarter moon phase (3.33 ± 1.12; Figure 3c) had the greatest mean (± SD) MaxN of megafauna.

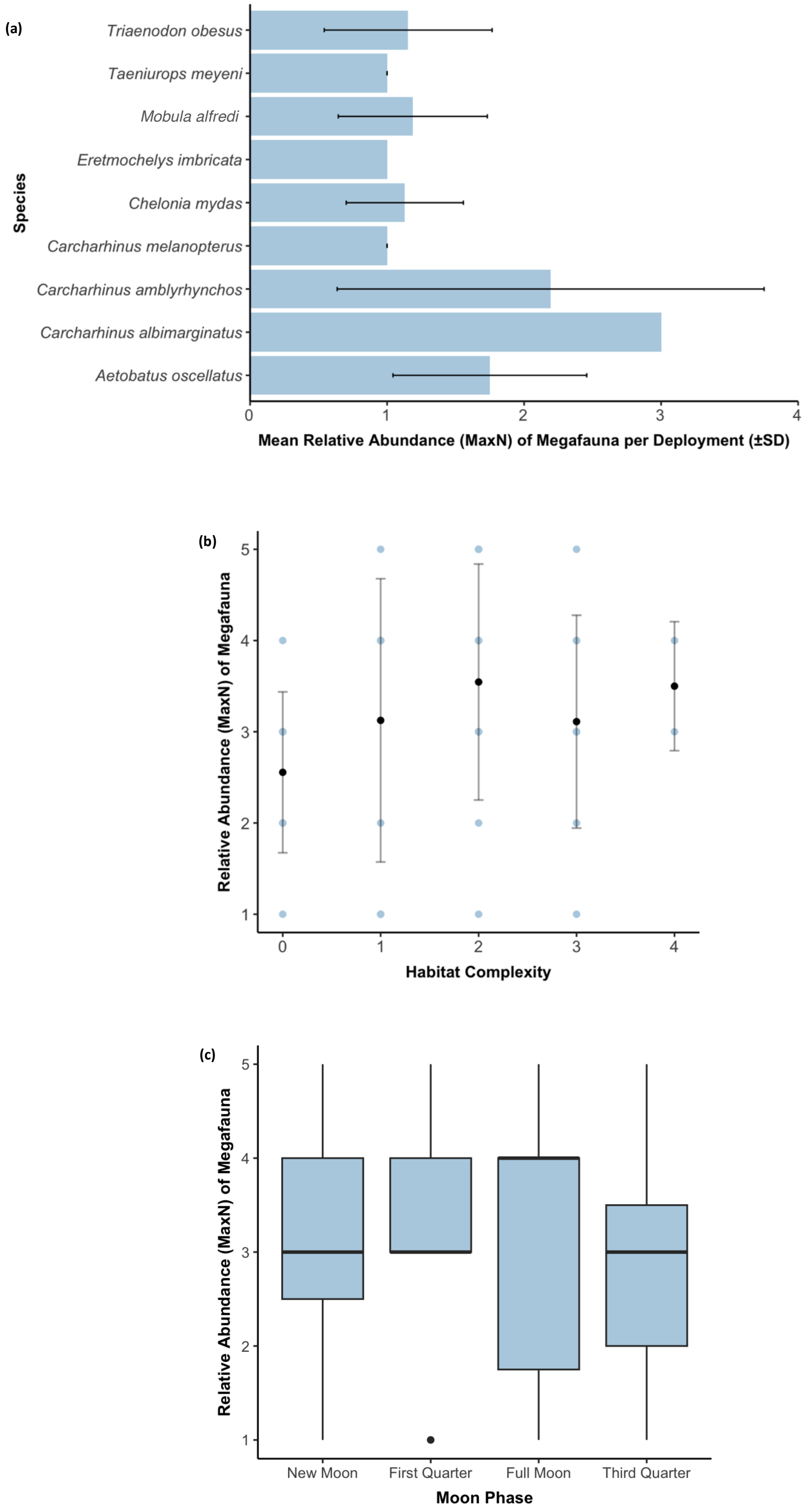

Figure 3. Examining the effects of habitat complexity and moon phase on the relative abundance (MaxN) of megafauna across cleaning stations in Laamu Atoll, Maldives. (a) Mean relative abundance (MaxN) of megafauna per deployment (± SD) (*n* = 39). Standard deviations (± SD) are indicated by black error bars. Note that a ± SD could not be calculated for the silvertip shark (*Carcharhinus albimarginatus*), as this species was recorded on only one deployment at Boduhuraa Beyru. The blotched fantail ray (*Taeniurops meyeni)* and blacktip reef shark (*Carcharhinus melanopterus*) had a ± SD of 0, as all values in the data set were the same. **(b)** Relative abundance (MaxN) of megafauna across cleaning station habitat complexities. Blue points show raw MaxN data. Black points show mean MaxN fitted with grey standard deviation (± SD) error bars. **(c)** Relative abundance (MaxN) of megafauna across moon phases. Boxes denote interquartile range; horizontal black lines indicate median and whiskers extend from 25th to 75th percentiles. Black points show outlying values.

Observed cleaning interaction duration of megafauna

A total of 525 cleaning interactions were recorded across the six cleaning stations in Laamu Atoll, Maldives. The two client species making up the greatest proportion of these interactions were the grey reef shark *(Carcharhinus amblyrhynchos*) and reef manta ray (*Mobula alfredi*) which accounted for 70.01% and 9.14% of observed cleaning interactions, respectively. The cleaner species making up the greatest proportion of these interactions were the slender sharksucker (*Echeneis naucrates*) and bluestreak cleaner wrasse (*Labroides dimidiatus*) which accounted for 59.20% and 35.80% of observed cleaning interactions, respectively. There are conflicting arguments as to whether the slender sharksucker (*Echeneis naucrates*) should be considered a cleaner organism. However, multiple studies have documented the cleaning benefits of this species and its mutualistic relationship with lemon sharks (*Negaprion brevirostris*) (Sazima, Moura and Rodrigues, 1999; Ritter and Amin, 2016). There was a statistically significant difference in cleaning interaction duration of megafauna between cleaning stations ($\chi^2_5 = 14.16$, $p < 0.05$; Figure 4a). Post-hoc testing revealed statistically significant differences in cleaning interaction duration between Fushi Kandu and Fonadhoo Beyru ($p = 0.01$; Figure 4a), Boduhuraa Beyru and Fushi Kandu ($p < 0.05$), Split Deep and Fushi Kandu ($p < 0.05$), Turtle Block and Fushi Kandu ($p < 0.05$), Yellow Block and Fushi Kandu ($p < 0.05$), and Yellow Block and Boduhuraa Beyru ($p = 0.03$). Yellow Block cleaning station (16.80 ± 20.7; Figure 4a) had the greatest mean (± SD) observed cleaning interaction duration (seconds). There was also a statistically significant difference in cleaning interaction duration between habitat complexities ($\chi^2_4 = 19.95$, $p < 0.05$; Figure 4b). Post-hoc testing revealed statistically significant differences in cleaning interaction duration between habitat complexity scores of 2 and 0 ($p < 0.05$), 3 and 0 ($p < 0.05$), and 3 and 1 ($p < 0.05$). Cleaning stations assigned a habitat complexity score of 3 (21.80 ± 27.20; Figure 4b) had the greatest mean (± SD) observed cleaning interaction duration (seconds). Lastly, there was a statistically significant difference in cleaning interaction duration of megafauna between moon phases ($\chi^2_3 = 30.06$, $p < 0.05$; Figure 4c). Post-hoc testing revealed statistically significant differences in cleaning interaction duration between the Third Quarter and Full Moon ($p = 0.02$) and Third Quarter and New Moon ($p = 0.05$) phases. The New Moon phase (19.30 ± 24.2; Figure 10) had the greatest mean (± SD) observed cleaning interaction duration (seconds).

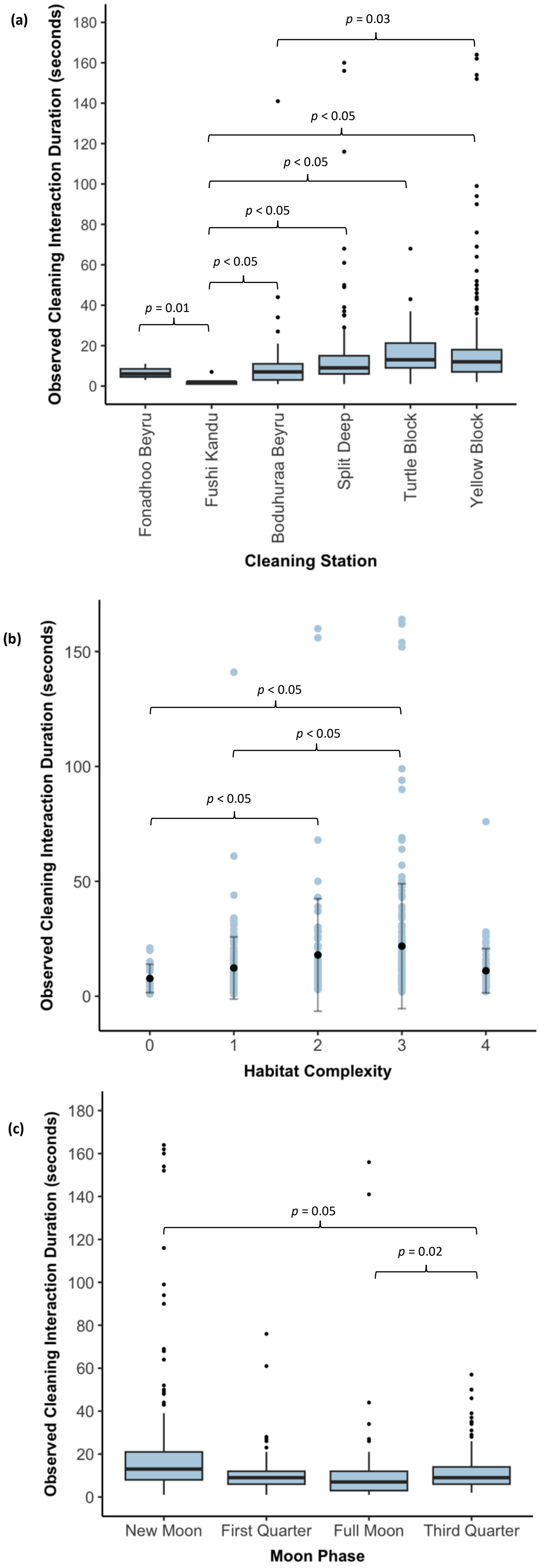

Figure 4. Examining the effects of cleaning station, habitat complexity, and moon phase on the observed cleaning interaction duration (seconds) of megafauna across cleaning stations in Laamu Atoll, Maldives. Statistically significant pairwise comparisons are indicated by black brackets. **(a)** Observed cleaning interaction duration (seconds) of megafauna across cleaning stations (*n* = 6) within all sampled deployment locations. Boxes denote interquartile range; horizontal black lines indicate median and whiskers extend from 25th to 75th percentiles. Black points show outlying values. **(b)** Observed cleaning interaction duration (seconds) of megafauna across cleaning station habitat complexities. Blue points show raw observed cleaning interaction duration data. Black points show mean observed cleaning interaction duration fitted with grey standard deviation (± SD) error bars. **(c)** Observed cleaning interaction duration (seconds) of megafauna across moon phases. Boxes denote interquartile range; horizontal black lines indicate median and whiskers extend from 25th to 75th percentiles. Black points show outlying values.

Discussion

Observed cleaning interaction duration of megafauna was the only predictor driven by cleaning station, habitat complexity, and moon phase. Whilst species richness was driven by cleaning station and habitat complexity, moon phase did not have a significant effect on the number of species identified per deployment. There was also no evidence of cleaning station, habitat complexity, or moon phase driving the relative abundance of megafauna across deployment locations. The wider implications of these findings have been discussed below and a series of key recommendations have been proposed to maximise research efforts and ensure future studies are conducted under best scientific practice.

Species richness

Species richness did not vary across cleaning stations in Laamu Atoll. In fact, 153 different species were identified across the deployment locations, suggesting that cleaning stations support a wide range of marine biodiversity despite the anthropogenic pressures they have faced over the last 30 years (Sharma and Sommer, 2022; Hilmi *et al*., 2023). The mass coral bleaching event of 1998 impacted up to 90% of shallow-water coral species in the Indian Ocean (Pisapia, Burn and Pratchett, 2019). However, the Maldives coral reefs recovered to pre-bleaching levels within 16 years and the species richness of cleaning stations identified in this study further highlights the recovery potential of these ecosystems (Montefalcone, Morri, and Bianchi, 2020). There was evidence of habitat complexity driving species richness across cleaning stations in Laamu Atoll. Structurally complex sites with varying relief had increased species richness, compared to sites with lower morphological diversity. These findings support the hypothesis that coral reef complexity is positively associated with species richness and suggest that these ecosystems play an important role in fish reproduction and recruitment (Denis *et al.,* 2017). Komyakova, Jones and Munday (2018) demonstrated this in a study investigating the effects of habitat complexity on fish species richness in Lizard Island lagoon, Australia. In this study, coral reef complexity explained up to 53.6% of variability in fish species richness (Komyakova, Jones and Munday, 2018). These findings have important management implications and suggest that habitat complexity may be an important indicator of cleaning station health and biodiversity. Previous studies have demonstrated this relationship and how cleaning stations with increased habitat complexity provide a greater number of refuge sites for new recruits and hence promote biodiversity on coral reefs (Beese, Mumby and Rogers, 2023). Lastly, species richness did not vary according to moon phase in Laamu Atoll. However, the greatest number of species were recorded during the New Moon phase. These findings are consistent with previous studies whereby researchers have recorded increased fish and macroinvertebrate species richness during the primary moon phase (Gutiérrez-Martínez *et al*., 2021). For example, Harrison *et al*. (2023) recorded increased spawning of spotted coral grouper (*Plectropomus maculatus*) in the Great Barrier Reef during the New Moon phase and recommended fishery closures during this period to protect commercially important stocks. We would expect increased species richness of cleaning stations following the New Moon phase, as coral reefs are important spawning grounds and provide individuals with increased protection from predation (Sektiana *et al*., 2022). However, previous studies on the effects of moon phase have focused primarily on commercial fisheries and how lunar cycling influences Catch Per Unit Effort (CPUE) (Tosunoglu *et* al., 2021; Han *et al*., 2022). Further research is required to examine the effects of moon phase on coral reef species richness and determine whether it influences other biological processes through tidal control.

When discussing the wider applications of this study, it is important to consider environmental variables that may have limited species identification. High turbidity was recognised as one of the most troubling parameters, as it obscured the colouration and markings of individuals. This limitation of UVC has been highlighted in previous studies and the use of bait is often proposed to overcome these conditions (King *et al*., 2018). However, BRUV surveys would not be suitable for this study, as they attract a disproportionate number of carnivorous species and the purpose of this study was to investigate cleaning symbioses and not feeding relationships (Whitmarsh, Huveneers and Fairweather, 2018; Rhodes *et al*., 2020). Fish body size was also recognised as a factor limiting species identification. However, this is a general limitation of RUV surveys and smaller benthic species are often underrepresented when using this method of UVC (Rolim *et al*., 2022).

Relative Abundance (MaxN) of Megafauna

Relative abundance of megafauna did not vary across cleaning stations in Laamu Atoll. These findings support the previous hypothesis that all cleaning stations support a wide range of marine biodiversity and suggest that megafauna do not exhibit a cleaning station preference. However, it is important to note that these observations were recorded from a sample of the population and findings should not be generalised across species. There was also no evidence of habitat complexity driving relative abundance of megafauna across cleaning stations in Laamu Atoll. This result was unexpected, as it has been previously described that structurally complex coral reefs support a greater number of megafauna from higher trophic levels (Sherman *et al*., 2023). Heudier, Mouillot and Mannocci (2023) demonstrated this in a study investigating the effects of coral reef habitat complexity on species richness and diversity of megafauna in Poé, New Caledonia. Researchers reported increased abundance of individuals from the Dasyatidae family at structurally complex sites (Heudier, Mouillot and Mannocci, 2023). These findings highlight the importance of assessing regional differences in cleaning station preference and suggest that further research is required to develop a more comprehensive understanding across taxa. In Laamu, the relative abundance of megafauna was greatest at cleaning stations assigned a habitat complexity score of 3. However, the insignificance of these findings may be explained by the VRI used to quantitatively estimate habitat complexity. There are several limitations of using this method and alternative 3D monitoring techniques have proven successful in calculating coral reef cover (House *et al*., 2018). Lastly, relative abundance of megafauna did not vary according to moon phase in Laamu Atoll. This result was unexpected, as several studies have demonstrated the effects of lunar cycling on manta ray abundance (Harris and Stevens, 2021; Carpenter *et al*., 2023). Barr and Abelson (2019) demonstrated this in a study investigating environmental drivers of giant oceanic manta ray (*Mobula birostris*) and reef manta ray (*Mobula alfredi*) visitation patterns at Manta Bowl cleaning station, Philippines. Researchers reported a statistically significant effect of moon phase on manta ray presence when the moon was equal to or less than half full (Barr and Abelson, 2019). These findings suggest that moon illumination plays a critical role in determining the frequency of cleaning interactions in the marine environment (Carpentier *et al.*, 2019; Gould, 2022). Similar findings were reported in this study, as relative abundance of megafauna was greatest during the First Quarter moon phase. These findings suggest that manta rays engage in cleaning symbioses during periods of low moon illumination due to decreased food availability and foraging opportunities (Barr and Abelson, 2019; Harris and Stevens, 2021). Additional environmental variables, such as water temperature and current speed, were not taken into account for this baseline assessment. However, they are likely to influence the relative abundance of megafauna and future research would benefit from incorporating these variables (Murie, Spencer and Oliver, 2020).

It is important to consider the limitations of using MaxN when discussing the insignificance of the findings outlined above. MaxN is widely used throughout scientific literature and provides a relative measure of abundance (Stobart *et* al., 2015; Logan *et al.*, 2017). However, previous studies have demonstrated that MaxN may underestimate the abundance of target species and generate conservative estimates (Denney *et al.*, 2017; Kilfoil *et al.*, 2017). Sherman *et al*. (2018) reported 2.4 and 1.1 fold decreases in abundance of oriental bluespotted maskrays (*Neotrygon orientalis*) and bluespotted fantail rays (*Taeniura lymma*) when using MaxN. These findings suggest that MaxN may not be a suitable metric for quantifying megafauna abundance and highlight how the findings of this study should be applied with caution. Alternative methods have been proposed to overcome this limitation, including counting the maximum number of distinct individuals (MaxIND) and using 360 degree devices to increase the sampling FOV (Sherman *et al.*, 2018; Currey-Randall *et al*., 2020; McIvor *et al*., 2022).

Observed cleaning interaction duration of megafauna

Observed cleaning interaction duration of megafauna varied across cleaning stations in Laamu Atoll. The longest cleaning interactions were recorded at Yellow Block, Split Deep and Turtle Block, suggesting that Hithadhoo Corner provides high quality cleaning services and that megafauna exhibit a strong preference due to the cleaner species present (Armstrong *et al*., 2021). However, it is important to remember that the greatest number of deployments were conducted at Hithadhoo Corner due to accessibility and resource availability. Future research would benefit from equal numbers of deployments across locations to reduce sampling bias. There was evidence of habitat complexity driving cleaning interaction duration of megafauna across cleaning stations in Laamu Atoll. The longest cleaning interactions were recorded at moderately complex sites, suggesting that habitat complexity is an important environmental factor determining the quality of cleaning symbioses. The decreased complexity score of this predictor may be explained by an environmental trade-off whereby client organisms prefer cleaning stations with greater habitat complexity, as they support larger populations of cleaner species. However, if cleaning stations are too complex, then cleaner or client organisms are unable to signal effectively and hence may exhibit a preference for moderately complex sites (Caves, Green and Johnson, 2018). Previous studies have demonstrated how coral reef substrate may influence cleaning station preference and interaction duration of megafauna (Whittey *et al*., 2021). Armstrong *et al*. (2021) demonstrated this in a study investigating the habitat use and cleaning station preference of reef manta rays (*Mobula alfredi*) around Lady Elliot Island, Australia. Researchers reported a strong preference for complex scleractinian coral reefs with outcrops (Armstrong *et al*., 2021). These protruding features attract a greater number of client species and facilitate effective positioning over cleaning stations (Armstrong *et al*., 2021; Whittey *et al*., 2021). These findings provide a potential explanation for the increased cleaning interaction duration of megafauna at complex sites. However, it is important that the Manta Trust monitors the health and structural integrity of cleaning stations across Laamu Atoll, as climate change is expected to impact hard corals most severely (Goulet and Goulet, 2021; Yasir Haya *et al*., 2023). The varied bleaching susceptibility of scleractinian corals further limits the recovery potential of these ecosystems and highlights an important area of research for the Manta Trust (Pisapia, Burn and Pratchett, 2019; Steinberg *et al*., 2022). Lastly, cleaning interaction duration of megafauna varied according to moon phase. The longest cleaning interactions were recorded during the New Moon phase. As previously mentioned, fish and macroinvertebrate species richness is greatest during this period (Gutiérrez-Martínez *et al*., 2021). These findings suggest that populations of cleaner fish may be greater during the New Moon phase and facilitate longer cleaning interactions. Several researchers have demonstrated the ecological benefits of high cleaner species richness. For example, Sun *et al*., (2015) reported increased juvenile fish recruitment as a result of high cleaner wrasse (*Labroides dimidiatus*) presence in the Great Barrier Reef, Australia. These findings suggest that high cleaner species richness plays an important role in marine ecosystem structuring and that these effects may be stronger during the New Moon phase (Sun *et al*., 2015). However, this field of research is relatively understudied and further research is required to determine whether there is a direct effect of moon phase on cleaning interaction duration of megafauna.

The ecological benefits of cleaning symbioses have been widely documented. However, there is a lack of research analysing the costs of cleaning symbioses at an individual and population level. Increased cleaning interaction rates have been shown to promote transmission of disease amongst client organisms (Brown *et al*., 2012; Narvaez *et al*., 2022). Indeed, Narvaez *et al*. (2021) demonstrated how cleaning symbioses can shift to parasitism and concluded that cleaning stations may act as “disease hotspots” and decrease marine ecosystem health when client organisms are used as transmitters of disease. This is a relatively new concept. However, future research would benefit from a greater understanding of the costs of cleaning symbioses given their prevalence in the marine environment.

Key Recommendations

1. RUVS enable researchers to gain insight into the species diversity of marine ecosystems and sample a range of depths and habitat types (Currey-Randall *et al*., 2020). However, data processing is time consuming and observer error is expected to increase with deployment duration (Erickson, Bugnot and Figueira, 2023). The first recommendation is to identify optimal RUV soak times. This will enable the Manta Trust to maximise sampling efforts and increase survey efficiency (Misa *et al*., 2016). Species accumulation curves are often used to identify optimal soak times and this would be a practical way for the organisation to utilise previous data (Devine *et* al., 2019; Mallet *et al*., 2021).
2. Structurally complex coral reefs support a wide range of marine biodiversity (Armstrong *et al*., 2021). The second recommendation is to monitor the habitat complexity of cleaning stations and prioritise protection of structurally complex sites, as they yield the greatest ecological benefits. Implementation of 3D modelling will provide the Manta Trust with an affordable coral reef

assessment tool and allow them to closely monitor cleaning station habitat degradation and make informed management decisions.

3. Unequal sampling efforts across deployment locations decreases statistical power (Serdar *et al*., 2021). The third recommendation is to conduct regular deployments across cleaning stations in Laamu Atoll and gather more data from Fushi Kandu, Fonadhoo Beyru and Boduhuraa Beyru. This will provide the Manta Trust with a more comprehensive understanding of cleaning station health and enable them to target conservation efforts more effectively.

Conclusion

This study provides a remarkable insight into the species diversity of six cleaning stations in Laamu Atoll, Maldives. It reports on the ecological role of cleaning symbioses and how cleaning interaction duration of megafauna is the only predictor driven by cleaning station, habitat complexity, and moon phase. These findings highlight how conservation efforts should be targeted towards protecting the structural integrity of cleaning stations in Laamu Atoll, as the quality of cleaning symbioses may decline if these sites experience further degradation. This is particularly important, as anthropogenic pressures on the marine environment have increased in recent years and projected levels of climate change are expected to impact coral reef ecosystems most severely through increased coral bleaching and outbreaks of disease (Cramer *et al*., 2020; Goreau and Hayes, 2021; Moullec *et al*., 2021).

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Supplementary Materials

Table S1. Habitat complexity scores of Remote Underwater Video (RUV) survey deployments ($n = 39$) conducted across cleaning stations in Laamu Atoll, Maldives. Values represent the number of deployments allocated each habitat complexity score at each cleaning station.

	Habitat complexity score				
Cleaning Station	**0**	**1**	**2**	**3**	**4**
Boduhuraa Beyru	0	2	0	0	0
Fonadhoo Beyru	1	0	0	0	0
Fushi Kandu	1	1	0	0	0
Split Deep	6	4	8	5	0
Turtle Block	1	0	3	0	0
Yellow Block	0	1	0	4	2

Table S2. Species identified across six cleaning stations in Laamu Atoll, Maldives ($n = 153$).

Common Name	**Scientific Name**	**Species Family**	**Species Order**
Pencilled surgeonfish	*Acanthurus dussumieri*	Acanthuridae	Acanthuriformes
White-spine surgeonfish	*Acanthurus leucocheilus*	Acanthuridae	Acanthuriformes
Powder-blue surgeonfish	*Acanthurus leucosternon*	Acanthuridae	Acanthuriformes
Eye-line surgeonfish	*Acanthurus nigricaudus*	Acanthuridae	Acanthuriformes
Night surgeonfish	*Acanthurus thompsoni*	Acanthuridae	Acanthuriformes
Yellow-fin surgeonfish	*Acanthurus xanthopterus*	Acanthuridae	Acanthuriformes
Red-flushed grouper	*Aethaloperca rogaa*	Serranidae	Perciformes
White-spotted eagle ray	*Aetobatus oscellatus*	Myliobatidae	Myliobatiformes
Diamond wrasse	*Anampses caeruleopunctatus*	Labridae	Labriformes
Speckled wrasse	*Anampses meleagrides*	Labridae	Labriformes
Small-tooth jobfish	*Aphareus furca*	Lutjanidae	Perciformes
Three-spot angelfish	*Apolemichthys trimaculatus*	Pomacanthidae	Perciformes
Green jobfish	*Aprion virescens*	Lutjanidae	Perciformes
Starry pufferfish	*Arothron stellatus*	Tetraodontidae	Tetradontiformes
Striped triggerfish	*Balistapus undulatus*	Balistidae	Tetradontiformes
Clown triggerfish	*Balistoides conspicillum*	Balistidae	Tetradontiformes
Titan triggerfish	*Balistoides viridescens*	Balistidae	Tetradontiformes
Adorned wrasse	*Biochoeres cosmetus*	Labridae	Perciformes
Coral hogfish	*Bodianus axillaris*	Labridae	Labriformes
Diana's hogfish	*Bodianus diana*	Labridae	Labriformes
Moon fusilier	*Caesio lunaris*	Caesionidae	Perciformes
Yellow-tail fusilier	*Caesio teres*	Caesionidae	Perciformes
Yellow-back fusilier	*Caesio xanthonota*	Caesionidae	Perciformes
Barred filefish	*Cantherhines dumerilii*	Monocanthidae	Tetradontiformes
Saddled pufferfish	*Canthigaster valentini*	Tetraodontidae	Tetradontiformes
Banded trevally	*Carangoides ferdau*	Carangidae	Perciformes
Giant trevally	*Caranx ignobilis*	Carangidae	Carangiformes
Blue-fin jack	*Caranx melampygus*	Carangidae	Carangiformes
Big-eye trevally	*Caranx sexfasciatus*	Carangidae	Carangiformes
Silvertip shark	*Carcharhinus albimarginatus*	Carcharhinidae	Carcharhiniformes

Grey reef shark	*Carcharhinus amblyrhynchos*	Carcharhinidae	Carcharhiniformes
Blacktip reef shark	*Carcharhinus melanopterus*	Carcharhinidae	Carcharhiniformes
Many-spined angelfish	*Centropyge multispinis*	Pomacanthidae	Perciformes
Peacock rock cod	*Cephalopholis argus*	Serranidae	Perciformes
Blackfin rock cod	*Cephalopholis nigripinnis*	Serranidae	Perciformes
Six-spot rock cod	*Cephalopholis sexmaculata*	Serranidae	Perciformes
Two-colour parrotfish	*Cetoscarus bicolor*	Scaridae	Labriformes
Spotted parrotfish	*Cetoscarus ocellatus*	Scaridae	Labriformes
Threadfin butterflyfish	*Chaetodon auriga*	Chaetodontidae	Perciformes
Eclipse butterflyfish	*Chaetodon bennetti*	Chaetodontidae	Perciformes
Head-band butterflyfish	*Chaetodon collare*	Chaetodontidae	Perciformes
Double-saddle butterflyfish	*Chaetodon falcula*	Chaetodontidae	Perciformes
Spotted butterflyfish	*Chaetodon guttatissimus*	Chaetodontidae	Perciformes
Brown butterflyfish	*Chaetodon kleinii*	Chaetodontidae	Perciformes
Racoon butterflyfish	*Chaetodon lunula*	Chaetodontidae	Perciformes
Meyer's butterflyfish	*Chaetodon meyeri*	Chaetodontidae	Perciformes
Pig-face butterflyfish	*Chaetodon oxycephalus*	Chaetodontidae	Perciformes
Chevroned butterflyfish	*Chaetodon trifascialis*	Chaetodontidae	Perciformes
Pinstriped butterflyfish	*Chaetodon trifasciatus*	Chaetodontidae	Perciformes
Yellow-head butterflyfish	*Chaetodon xanthocephalus*	Chaetodontidae	Perciformes
Napoleonfish	*Cheilinus undulatus*	Labridae	Labriformes
Green sea turtle	*Chelonia mydas*	Cheloniidae	Testudines
Shabby parrotfish	*Chlorurus sordidus*	Scaridae	Labriformes
Sheephead parrotfish	*Chlorurus strongylocephalus*	Scaridae	Labriformes
Two-tone puller	*Chromis dimidiata*	Pomacentridae	Perciformes
Double-bar puller	*Chromis opercularis*	Pomacentridae	Perciformes
Pemba puller	*Chromis pembae*	Pomacentridae	Perciformes
Green puller	*Chromis viridis*	Pomacentridae	Perciformes
Weber's puller	*Chromis weberi*	Pomacentridae	Perciformes
Spotted hawkfish	*Cirrhitichthys oxycephalus*	Cirrhitidae	Perciformes
Two-spot bristletooth	*Ctenochaetus binotatus*	Acanthuridae	Acanthuriformes
Fine-lined bristletooth	*Ctenochaetus striatus*	Acanthuridae	Perciformes
Indian humbug	*Dascyllus carneus*	Pomacentridae	Perciformes
Spotted porcupinefish	*Diodon hystrix*	Diodontidae	Tetradontiformes
Slender suckerfish	*Echeneis naucrates*	Echeneidae	Carangiformes
Two-colour combtooth blenny	*Ecsenius bicolor*	Blennidae	Perciformes
Little combtooth blenny	*Ecsenius minutus*	Blennidae	Perciformes
Rainbow runner	*Elagatis bipinnulatus*	Carangidae	Carangiformes
Sling-jaw wrasse	*Epibulus insidiator*	Labridae	Perciformes
Small-spotted grouper	*Epinephelus coeruleopunctatus*	Serranidae	Perciformes
Blacktip grouper	*Epinephelus fasciatus*	Serranidae	Perciformes
Flower grouper	*Epinephelus fuscoguttatus*	Serranidae	Perciformes
White-speckled grouper	*Epinephelus ongus*	Serranidae	Perciformes
Snout-spots grouper	*Epinephelus polyphekadion*	Serranidae	Perciformes
Hawksbill sea turtle	*Eretmochelys imbricata*	Cheloniidae	Testudines
Smooth flutemouth	*Fistularia commersonii*	Fistulariidae	Syngnathiformes
Gold-spot emperor	*Gnathodentex aurolineatus*	Lethrinidae	Perciformes

Bird wrasse	*Gomphosus caeruleus*	Labridae	Labriformes
Checkerboard wrasse	*Hemitautoga hortulanus*	Labridae	Perciformes
Reef bannerfish	*Heniochus acuminatus*	Chaetodontidae	Perciformes
Phantom bannerfish	*Heniochus pleurotaenia*	Chaetodontidae	Perciformes
Singular bannerfish	*Heniochus singularis*	Chaetodontidae	Perciformes
Longnose parrotfish	*Hipposcarus harid*	Scaridae	Labriformes
Snubnose rudderfish	*Kyphosus cinerascens*	Kyphosidae	Perciformes
Two-colour cleaner wrasse	*Labroides bicolor*	Labridae	Perciformes
Blue-streak cleaner wrasse	*Labroides dimidiatus*	Labridae	Labriformes
V-tail tubelip wrasse	*Labropsis xanthonota*	Labridae	Perciformes
Orange-finned emperor	*Lethrinus erythracanthus*	Lethrinidae	Perciformes
Spangled emperor	*Lethrinus nebulosus*	Lethrinidae	Perciformes
Long-nose emperor	*Lethrinus olivaceus*	Lethrinidae	Perciformes
Red bass	*Lutjanus bohar*	Lutjanidae	Perciformes
Black-tail snapper	*Lutjanus fulvus*	Lutjanidae	Perciformes
Humpback snapper	*Lutjanus gibbus*	Lutjanidae	Perciformes
Blue-striped snapper	*Lutjanus kasmira*	Lutjanidae	Perciformes
One-spot snapper	*Lutjanus monostigma*	Lutjanidae	Perciformes
Midnight snapper	*Macolor macularis*	Lutjanidae	Perciformes
Black snapper	*Macolor niger*	Lutjanidae	Perciformes
Reef manta ray	*Mobula alfredi*	Mobulidae	Myliobatiformes
Large-eye bream	*Monotaxis grandoculis*	Lethrinidae	Perciformes
Shadowfin soldierfish	*Myripristis adusta*	Holocentridae	Holocentriformes
Yellow-fin soldierfish	*Myripristis berndti*	Holocentridae	Holocentriformes
Epaulette soldierfish	*Myripristis kuntee*	Holocentridae	Holocentriformes
Splendid soldierfish	*Myripristis melanosticta*	Holocentridae	Holocentriformes
Crimson soldierfish	*Myripristris murdjan*	Holocentridae	Holocentriformes
Spotted unicornfish	*Naso brevirostris*	Acanthuridae	Acanthuriformes
Orange-spine unicornfish	*Naso elegans*	Acanthuridae	Perciformes
Sleek unicornfish	*Naso hexacanthus*	Acanthuridae	Acanthuriformes
Big-nose unicornfish	*Naso vlamingii*	Acanthuridae	Acanthuriformes
Threadfin basslet	*Nemanthias carberryi*	Serranidae	Perciformes
Yellow boxfish	*Ostracion cubicus*	Ostraciidae	Tetradontiformes
Ring-eye hawkfish	*Paracirrhites arcatus*	Cirrhitidae	Perciformes
Forster's hawkfish	*Paracirrhites forsteri*	Cirrhitidae	Perciformes
Yellow-saddle goatfish	*Parupeneus cyclostomus*	Mullidae	Mulliformes
Long-barbel goatfish	*Parupeneus macronema*	Mullidae	Perciformes
Double-bar goatfish	*Parupeneus trifasciatus*	Mullidae	Mulliformes
Tube-worm blenny	*Plagiotremus rhinorhynchos*	Blennidae	Perciformes
Rounded batfish	*Platax orbicularis*	Ephippidae	Moroniformes
Tall-fin batfish	*Platax teira*	Ephippidae	Moroniformes
Giant sweetlips	*Plectorhinchus albovittatus*	Haemulidae	Perciformes
Brown sweetlips	*Plectorhinchus gibbosus*	Haemulidae	Perciformes
Oriental sweetlips	*Plectorhinchus vittatus*	Haemulidae	Perciformes
Harlequin sweetlips	*Plectrohinchus chaetodonoides*	Haemulidae	Perciformes
Squaretail coral grouper	*Plectropomus areolatus*	Serranidae	Perciformes
Black-saddle coral grouper	*Plectropomus laevis*	Serranidae	Perciformes

Emperor angelfish	*Pomacanthus imperator*	Pomacanthidae	Perciformes
Blue-face angelfish	*Pomacanthus xanthometopon*	Pomacanthidae	Perciformes
Indian damsel	*Pomacentrus indicus*	Pomacentridae	Perciformes
Yellow-back basslet	*Pseudanthias bicolor*	Serranidae	Perciformes
Yellow-tail basslet	*Pseudanthias evansi*	Serranidae	Perciformes
Orange basslet	*Pseudanthias squamipinnis*	Serranidae	Perciformes
Chiseltooth wrasse	*Pseudodax moluccanus*	Labridae	Labriformes
Blue-dash fusilier	*Pterocaesio tile*	Caesionidae	Perciformes
Regal angelfish	*Pygoplites dicanthus*	Pomacanthidae	Perciformes
White-tail squirrelfish	*Sargocentron caudimaculatum*	Holocentridae	Holocentriformes
Sabre squirrelfish	*Sargocentron spiniferum*	Holocentridae	Holocentriformes
Bridled parrotfish	*Scarus frenatus*	Scaridae	Labriformes
Blue-barred parrotfish	*Scarus ghobban*	Scaridae	Labriformes
Rosy-cheek parrotfish	*Scarus psittacus*	Scaridae	Labriformes
Ember parrotfish	*Scarus rubroviolaceus*	Scaridae	Labriformes
Three-colour parrotfish	*Scarus tricolor*	Scaridae	Labriformes
Double-spotted queenfish	*Scomberoides lysan*	Carangidae	Carangiformes
Coral rabbitfish	*Siganus corallinus*	Siganidae	Perciformes
Starry rabbitfish	*Siganus laques*	Siganidae	Perciformes
Big-eye barracuda	*Sphyraena forsteri*	Sphyraenidae	Istiophoriformes
Chevron barracuda	*Sphyraena putnamae*	Sphyraenidae	Perciformes
Boomerang triggerfish	*Sufflamen bursa*	Balistidae	Tetradontiformes
Blotched fantail ray	*Taeniurops meyeni*	Dasyatidae	Myliobatiformes
Two-tone wrasse	*Thalassoma amblycephalum*	Labridae	Perciformes
Moon wrasse	*Thalassoma lunare*	Labridae	Labriformes
Snub-nose pompano	*Trachinotus blochii*	Carangidae	Carangiformes
Whitetip reef shark	*Triaenodon obesus*	Carcharhinidae	Carcharhiniformes
Moorish idol	*Zanclus cornutus*	Zanclidae	Acanthuriformes
Sail-fin surgeonfish	*Zebrasoma desjardinii*	Acanthuridae	Acanthuriformes

Table S3. Species identified at one cleaning station in Laamu Atoll, Maldives (*n* = 132).

Common Name	Scientific Name	Species Family	Species Order	Cleaning Station
Pencilled surgeonfish	*Acanthurus dussumieri*	Acanthuridae	Acanthuriformes	Split Deep
Diamond wrasse	*Anampses caeruleopunctatus*	Labridae	Labriformes	Split Deep
Speckled wrasse	*Anampses meleagrides*	Labridae	Labriformes	Split Deep
Three-spot angelfish	*Apolemichthys trimaculatus*	Pomacanthidae	Perciformes	Yellow Block
Starry pufferfish	*Arothron stellatus*	Tetraodontidae	Tetradontiformes	Split Deep
Barred filefish	*Cantherhines dumerilii*	Monocanthidae	Tetradontiformes	Split Deep
Saddled pufferfish	*Canthigaster valentini*	Tetraodontidae	Tetradontiformes	Split Deep
Giant trevally	*Caranx ignobilis*	Carangidae	Carangiformes	Boduhuraa Beyru
Silvertip shark	*Carcharhinus albimarginatus*	Carcharhinidae	Carcharhiniformes	Boduhuraa Beyru
Six-spot rock cod	*Cephalopholis sexmaculata*	Serranidae	Perciformes	Split Deep
Double-saddle butterflyfish	*Chaetodon falcula*	Chaetodontidae	Perciformes	Split Deep
Pig-face butterflyfish	*Chaetodon oxycephalus*	Chaetodontidae	Perciformes	Split Deep

Chevroned butterflyfish	*Chaetodon trifascialis*	Chaetodontidae	Perciformes	Split Deep
Indian humbug	*Dascyllus carneus*	Pomacentridae	Perciformes	Boduhuraa Beyru
Spotted porcupinefish	*Diodon hystrix*	Diodontidae	Tetradontiformes	Split Deep
Blacktip grouper	*Epinephelus fasciatus*	Serranidae	Perciformes	Split Deep
Snout-spots grouper	*Epinephelus polyphekadion*	Serranidae	Perciformes	Split Deep
Hawksbill sea turtle	*Eretmochelys imbricata*	Cheloniidae	Testudines	Split Deep
Smooth flutemouth	*Fistularia commersonii*	Fistulariidae	Syngnathiformes	Fushi Kandu
Gold-spot emperor	*Gnathodentex aurolineatus*	Lethrinidae	Perciformes	Turtle Block
Snubnose rudderfish	*Kyphosus cinerascens*	Kyphosidae	Perciformes	Split Deep
V-tail tubelip wrasse	*Labropsis xanthonota*	Labridae	Perciformes	Yellow Block
Black-tail snapper	*Lutjanus fulvus*	Lutjanidae	Perciformes	Split Deep
Yellow boxfish	*Ostracion cubicus*	Ostraciidae	Tetradontiformes	Split Deep
Forster's hawkfish	*Paracirrhites forsteri*	Cirrhitidae	Perciformes	Turtle Block
Yellow-saddle goatfish	*Parupeneus cyclostomus*	Mullidae	Mulliformes	Split Deep
Long-barbel goatfish	*Parupeneus macronema*	Mullidae	Perciformes	Fonadhoo Beyru
Indian damsel	*Pomacentrus indicus*	Pomacentridae	Perciformes	Split Deep
Chiseltooth wrasse	*Pseudodax moluccanus*	Labridae	Labriformes	Split Deep
Rosy-cheek parrotfish	*Scarus psittacus*	Scaridae	Labriformes	Split Deep
Double-spotted queenfish	*Scomberoides lysan*	Carangidae	Carangiformes	Boduhuraa Beyru
Coral rabbitfish	*Siganus corallinus*	Siganidae	Perciformes	Fushi Kandu

Table S4. Megafauna species identified across six cleaning stations in Laamu Atoll, Maldives (*n* = 9).

Common Name	Scientific Name	Species Family	Species Order
White-spotted eagle ray	*Aetobatus oscellatus*	Myliobatidae	Myliobatiformes
Silvertip shark	*Carcharhinus albimarginatus*	Carcharhinidae	Carcharhiniformes
Grey reef shark	*Carcharhinus amblyrhynchos*	Carcharhinidae	Carcharhiniformes
Blacktip reef shark	*Carcharhinus melanopterus*	Carcharhinidae	Carcharhiniformes
Green sea turtle	*Chelonia mydas*	Cheloniidae	Testudines
Hawksbill sea turtle	*Eretmochelys imbricata*	Cheloniidae	Testudines
Reef manta ray	*Mobula alfredi*	Mobulidae	Myliobatiformes
Blotched fantail ray	*Taeniurops meyeni*	Dasyatidae	Myliobatiformes
Whitetip reef shark	*Triaenodon obesus*	Carcharhinidae	Carcharhiniformes