Diurnal predator attacks indirectly affect overnight retention of restocked *Diadema antillarum* on artificial reefs

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The long-spined sea urchin *Diadema antillarum* controls reef dynamics by grazing on algae, and increasing coral recruitment. Populations of *D. antillarum* never recovered after a mass-die off in 1983 and 1984 and numbers were further reduced by a more recent die-off in 2022. To restore grazing pressure and thereby the resilience of Caribbean coral reefs, multiple *D. antillarum* restocking efforts have been performed. Although results vary, the relatively low retention is one of the reasons restocking is not considered more often. If causes for the low retention will be identified, suitable measures can be taken to increase restocking success of *D. antillarum*. In this study, we monitored restocked lab-reared and wild juvenile *D. antillarum* on artificial reefs around Saba, Caribbean Netherlands. To assess the retention of *D. antillarum* over time, we conducted diver surveys and used remote underwater photo time lapse during daylight. Retention of uncaged lab-reared and wild *D. antillarum* decreased steadily and was low after 10 days. In total, 138 predator-prey interactions were recorded, of which 99% were conducted by the queen triggerfish *Balistes vetula*. Other predators showed limited interest in the restocked *D. antillarum.* None of the predator-prey interactions was successful, which suggests that artificial reefs with incorporated shelters may be suitable for juveniles as daytime refuge. However, *D. antillarum* that were often attacked during the day, often vacated their shelter during the night. As no *D. antillarum* were found back on surrounding reefs, we expect that they moved off the artificial reefs in search for better shelter and were predated during the night. Our remote photos revealed that wild *D. antillarum* were attacked significantly more than lab-reared *D. antillarum*, possibly because the wild urchins were slightly bigger, but this did not significantly affect retention. Future restocking should be performed on natural or artificial reefs with deeper shelters, so *D. antillarum* can retract further into their crevice, and should include night-time monitoring to identify the remaining unknown factors that cause low retention, including the main nocturnal predators. This knowledge is urgently needed for coral reef managers so they

can increase *D. antillarum* restocking success by selecting reefs with a lower predator density, protect urchins during an acclimatization period and/or conduct temporary predator control measures.

Diurnal predator attacks indirectly affect overnight retention of restocked *Diadema antillarum* on artificial reefs

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Abstract

The long-spined sea urchin *Diadema antillarum* controls reef dynamics by grazing on algae, and increasing coral recruitment. Populations of *D. antillarum* never recovered after a mass-die off in 1983 and 1984 and numbers were further reduced by a more recent die-off in 2022. To restore grazing pressure and thereby the resilience of Caribbean coral reefs, multiple *D. antillarum* restocking efforts have been performed. Although results vary, the relatively low retention is one of the reasons restocking is not considered more often. If causes for the low retention will be identified, suitable measures can be taken to increase restocking success of *D. antillarum*. In this study, we monitored restocked lab-reared and wild juvenile *D. antillarum* on artificial reefs around Saba, Caribbean Netherlands. To assess the retention of *D. antillarum* over time, we conducted diver surveys and used remote underwater photo time lapse during daylight. Retention of uncaged lab-reared and wild *D. antillarum* decreased steadily and was low after 10 days. In total, 138 predator-prey interactions were recorded, of which 99% were conducted by the queen triggerfish *Balistes vetula*. Other predators showed limited interest in the restocked *D. antillarum*. None of the predator-prey interactions was successful, which suggests that artificial reefs with incorporated shelters may be suitable for juveniles as daytime refuge. However, *D. antillarum* that were often attacked during the day, often vacated their shelter during the night. As no *D. antillarum* were found back on surrounding reefs, we expect that they moved off the artificial reefs in search for better shelter and were predated during the night. Our remote photos revealed that wild *D. antillarum* were attacked significantly more than lab-reared *D. antillarum*, possibly because the wild urchins were slightly bigger, but this did not significantly affect retention. Future restocking should be performed on natural or artificial reefs with deeper shelters, so *D. antillarum* can retract further into their crevice, and should include night-time monitoring to identify the remaining unknown factors that cause low retention, including the main nocturnal predators. This knowledge is urgently needed for coral reef managers so they can increase *D. antillarum* restocking success by selecting reefs with a lower predator density, protect urchins during an acclimatization period and/or conduct temporary predator control measures.

Key words:

reef restoration, coral reef, Caribbean, sea urchin, predation

Introduction

The long-spined sea urchin *Diadema antillarum* was once a ubiquitous species on Caribbean coral reefs. High densities of 12 to 71 m^{-2} were found on reefs and other habitats throughout the region (Randall et al., 1964; Sammarco, 1982; Bak et al., 1984). *D. antillarum* is considered a

keystone herbivore as it structures the benthic community through its gregarious grazing behaviour. Between 1983 and 1984, 95-99% of all *D. antillarum* were killed during one of the most extensive and severe die-offs ever recorded for a marine invertebrate (Lessios et al., 1984a, 1984b; Hughes et al., 1985; Hunte et al., 1986; Levitan et al., 2014). Without other herbivores to fill the niche (Mumby et al., 2006; Dell et al., 2020), macroalgae became the dominant benthic group on many Caribbean coral reefs (Hughes et al., 1985; Carpenter, 1986; Lessios, 1988). Other stressors such as disease outbreaks and hurricanes reduced coral cover by as much as 50% (Hughes, 1994; Jackson et al., 2014; Cramer et al., 2020). The emptied space was quickly overgrown by macroalgae and other benthic organisms such as cyanobacteria (Bakker et al., 2017) and peyssonnelids (Williams and Garcia-Sais, 2020; Wilson et al., 2020; Stockton and Edmunds, 2021), which all inhibit coral recruitment (Lessios, 1988; McCook et al., 2001; Kuffner et al., 2006). This resulted in coral recruitment failure and a decreased resilience of Caribbean coral reefs (Bellwood et al., 2004).

In the decades after the die-off, *D. antillarum* recovery remained slow. In 2016, Lessios (2016) estimated the *D. antillarum* density as 8.5 times less dense than before the 1983-1984 die-off. The few recovered *D. antillarum* populations have been linked to reduced macroalgae cover (Edmunds and Carpenter, 2001; Myhre and Acevedo-Gutiérrez, 2007), increased coral recruitment (Carpenter and Edmunds, 2006), survival and growth (Idjadi et al., 2010) and ultimately, higher coral cover (Myhre and Acevedo-Gutiérrez, 2007). Active restoration of *D. antillarum* has therefore become a top priority in Caribbean coral reef management (Bellwood et al., 2004), especially because a new die-off reduced population densities across the Caribbean in 2022 (Hylkema et al. 2023). Approaches to restore *D. antillarum* include restocking individuals (Chiappone et al., 2006; Nedimyer and Moe, 2006; Dame, 2008) or Assisted Natural Recovery (ANR) in which suitable settlement substrate for *D. antillarum* larvae is supplied on the reef (Hylkema et al. 2022). Individuals for restocking can be acquired through culture from gametes (Pilnick et al., 2021; Wijers et al., 2023) and in-situ collection of settlers (Williams, 2018, 2022), but most restocking attempts have been performed by translocating individuals from naturally recovered areas to experimental plots (Chiappone et al., 2006; Nedimyer and Moe, 2006; Maciá et al., 2007; Burdick, 2008; Dame, 2008).

Some restocking attempts recorded retention of *D. antillarum* on experimental reefs of up to 52% after 3 to 6 weeks (Maciá et al., 2007; Dame, 2008; Williams, 2018). However, most restocking attempts had relatively few or no retaining *D. antillarum* after 3.5 to 12 months (Chiappone et al., 2006; Nedimyer and Moe, 2006; Burdick, 2008; de Breuyn, 2021). Most authors point toward predation (The Nature Conservancy, 2004; Chiappone et al., 2006; Nedimyer and Moe, 2006; Burdick, 2008), emigration (Maciá et al., 2007; Williams, 2018), or a combination of both (Dame, 2008; Wynne, 2008; Williams, 2022) as potential causes for the decline of restocked *D. antillarum*. Predation may be due to high predation pressure by fishes (Harborne et al., 2009), low fitness of lab-reared *D. antillarum* (Sharp et al., 2018) or a lack of available refuge (Bodmer et al., 2015), while emigration may be triggered by low food availability (Vadas, 1977) or predator avoidance behaviour (Snyder and Snyder, 1970). With the

positive effects of recovered *D. antillarum* populations, the slow recovery in other places as well as the few successful restocking attempts, the need for successful *D. antillarum* restocking practices is high and the key factors determining retention must be identified.
On Saba, Caribbean Netherlands, a restocking experiment was conducted with 147 lab-reared juveniles (de Breuyn, 2021), which were introduced on artificial reefs with suitable shelters, as recommended by Delgado and Sharp (2021). As with multiple other restocking attempts, retention was low and the cause unknown (de Breuyn, 2021). Because spines with tissue chunks were observed as fast as one hour after introduction, the author pointed towards a diurnal predator as the most important factor affecting retention, but no actual attacks were observed.
The aim of the current study was to identify the main predators of restocked *D. antillarum* on artificial reefs on Saba. We hypothesize that diurnal predation is the main cause for low retention of *D. antillarum* at this location. As susceptibility to predation might differ between lab-reared and wild individuals (Sharp et al., 2018; Brundu et al., 2020), individuals from both sources were introduced on standardized artificial reefs and monitored intensively using time lapse cameras. Based on Sharp et al. (2018) and Brundu et al. (2020) we hypothesize that lab-reared *D. antillarum* have a lower retention than wild conspecifics. Our study will increase insight in the main factors affecting retention of restocked *D. antillarum* and determine if lab-reared and wild *D. antillarum* are suitable for restocking.

Materials & Methods

We conducted our field experiments at Big Rock Market (N: 17.36772, W: 063.14264) which lies South of Saba, Caribbean Netherlands, within the Saba National Marine Park (Fig. 1). Our study site was at a depth of 19 m and in the proximity of a previous study site, where *D. antillarum* restocking was unsuccessful due to one or more unidentified predators (de Breuyn, 2021).

2.1 Experimental set-up

Twelve Moreef (Modular Restoration Reef, www.moreef.com) artificial reef modules were set out in two rows of six on a large sand patch with nearby patch reefs (Fig. 2a). The Moreefs were spaced one meter apart, which was the largest distance possible while allowing two reefs being monitored by a single camera, as only four camera setups were available. The four reefs on the outside of the rows were placed in cages made from chicken wire with a mesh size of 1.3 cm and functioned as control (Fig. 2b).

Moreef modules (height=30 cm, diameter=60 cm) were made from concrete in August 2020. Each Moreef module contains eight blind shelters, two tunnel shelters and numerous micro-shelters (Fig. 3). The artificial reefs were deployed in September 2020 and repositioned for the current experiment in March 2021.

Treatments consisted of lab-reared or wild juvenile *D. antillarum* and were assigned to the artificial reef modules in an alternating order to evenly divide the groups onto the two rows. The cages at each end of the rows were closed after introduction of *D. antillarum* and served as a control to monitor the survival of *D. antillarum* when emigration and predation were excluded. On 13 April 2021, four *D. antillarum* were placed per artificial reef module, one in each blind shelter facing the camera. In total, 48 *D. antillarum* were introduced (24 wild and 24 lab-reared) of which 16 were placed on the four caged artificial reef modules. The lab-reared *D. antillarum* were collected as settlers and head-started in a land-based nursery following the approach of Williams (2016). Wild individuals were translocated from the dive site Diadema City (Fig. 1) where a former breakwater harbored the largest population of *D. antillarum* around Saba at the time of this study. To keep the sizes of wild and lab-reared *D. antillarum* as similar as possible, we aimed to select wild individuals within the size range of lab-reared *D. antillarum* from the nursery (17-33 mm test size). However, even when using the smallest collected recruits, the average (±SD) test size of wild individuals was 32.6 ± 5.5 mm and slightly larger than the 24.8 ± 4.0 mm for lab-reared *D. antillarum*.

2.2 Retention surveys and remote camera footage

We conducted retention surveys on 1, 2, 3, 6, 7 and 10 days after restocking between 8 and 9am. During retention surveys each shelter was inspected for *D. antillarum*. To determine behaviour of *D. antillarum* and to identify predators all eight uncaged reefs were monitored with four remote underwater camera setups throughout 10 days. Each camera setup consisted of a GoPro 8 (GoPro, Inc.) inside a 4" watertight cylinder (Blue Robotics Inc.). Two power banks (V75 USB Battery Pack, Voltaic Systems) with a total capacity of 19,200 mAh per camera were enclosed. The setups were placed on a stand on which the camera setups could easily be attached and reattached at 55cm above the seabed. The cameras setups were installed simultaneously with the introduction of *D. antillarum* at the start of the experiment (day 0). The setups were installed to photograph the blind shelters with introduced *D. antillarum* and a surrounding margin of one meter to be able to monitor any activity on the sand and in the surrounding water column of the artificial reefs.

We managed to have cameras running at time lapse photo intervals of five seconds in a wide-angle setting for an average of 45 hours per deployment. All cameras were removed on day 2 and day 5 to be reinstalled on day 3 and day 7 respectively. This resulted in approximately 503 hours of survey time during the day (see Fig. S1 for timeline graph). One limitation of this study is that no underwater lights with adequate battery power were available, preventing night-time observations.

2.3 Picture analysis

Four camera setups took photos during three camera installations throughout 10 days. This resulted in approximately 32,400 photos per camera per installation and an overall total of

388,800 photos (four cameras multiplied by three runs). Pictures taken within ten minutes after retention surveys or camera deployments were excluded from analysis. Pictures taken at night were also excluded as they were entirely black. We manually analysed 194,400 pictures. For analysis, each picture was carefully searched for known predators of *D. antillarum* and for *D. antillarum* outside of their shelter space. The list of predators was based on Randall et al. (1964) and included black margate *Anisotremus surinamensis,* white margate *Haemulon album,* Spanish grunt *Haemulon macrostomum,* Caesar grunt *Haemulon carbonarium,* white grunt *Haemulon plumierii,* bluestriped grunt *Haemulon Sciurus,* permit *Trachinotus falcatus,* jolthead porgy *Calamus bajonado,* saucereye porgy *Calamus calamus,* Spanish hogfish *Bodianus rufus,* Caribbean spiny lobster *Panulirus argus,* queen triggerfish *Balistes vetula* bandtail puffer *Sphoeroides spengleri* and the spotted porcupine fish *Diodon hysterix*. The list of predators was supplemented with the spotted spiny lobster *Panulirus guttatus*, which was reported as a *D. antillarum* predator by Kintzing and Butler (2014).

Sightings were coded according to predefined codes (Table 1) of which examples can be seen in Fig. 4. Predator sightings were coded 1-7 and include a code for a predator-prey interaction on the reef (code 4) and off the reef (code 6), as well as a code for a predator feeding on *D. antillarum* (code 7). Codes 8 and 9 relate to *D. antillarum* outside of their shelter space without the presence of a predator. It was not feasible to observe the actual attack inside the shelter on picture, due to *D. antillarum* retracting into the shelter and predators following, blocking the view of the cameras. We therefore coded these potential attacks as "Interaction between *D. antillarum* predator and *D. antillarum* on the artificial reef" (code 4). Pictures were only attributed to a single and most precise code describing the action, so a picture with a predator interacting with *D. antillarum* in the shelter was only attributed to code 4 and not to code 1, 2 or 3. We installed cameras opposite of each other, so both cameras had two artificial reefs in the front and two in the back of the picture, to account for actions at the back of the artificial reefs. Codes 2-9 were only recorded for the two artificial reefs directly in front of the respective camera, avoiding double counts of the cameras opposite. We cannot exclude the possibility that code 1 had double counts as the distance was too inaccurate to assign the sighting to a specific Moreef.

2.4 Roving diver survey

To determine the presence of predators on the surrounding reefs, a roving diver visual survey was conducted after completion of the retention count on day 6. No cameras were running during that time frame, preventing interference with the camera footage of the experiment. We based the survey on the fish roving diver technique, which considers presence/absence data as well as frequencies of fish species (Hill and Wilkinson, 2004), and adapted it by only including predators relevant to *D. antillarum* (Randall et al., 1964; Kintzing and Butler, 2014). The starting point of the survey was the centre of the experimental plot at location BRM. Three scuba divers

systematically inspected the reefs within a 200 m radius from the experimental plots for 30 minutes and recorded all predators of *D. antillarum* as well as their size.

2.5 Statistical analysis

A Generalized Linear Mixed Model (GLMM) was used to assess the effect of source (factor: lab-reared or wild), caging (factor: caged or uncaged) and day of the experiment (covariate) on the retention of *D. antillarum* (response variable, modelled as number of urchins alive, number of urchins dead). As urchins alive were a proportion of the initial number of restocked individuals, a binomial distribution was used. Models were fit using the glmer function in the R package "lme4" (Bates et al., 2014). To account for daily repeated surveys on the same reefs, reef ID was included as random factor. For statistical inference, likelihood ratio tests (LRT) were performed using the drop1 function (Zuur et al. 2009).

Generalized Linear Models (GLMs) were used to assess the effect of treatment (fixed factor) on the number of times a predator was within 10 cm (code 3) and interacted with the *D. antillarum* (code 4). Model validation was performed according to Zuur et al. (2009). Initial models were fit with a Poisson distribution (glm function with family=poisson in the R package "lme4") but turned out to be overdispersed. This was resolved by using a negative-binomial distribution (glm.nb function in the R package "MASS"). Likelihood ratio tests (LRT) were performed for statistical inference of the fixed factors using the drop1 function.

To test if the number of interactions recorded for a specific shelter affected the respective shelter to be vacated the next day, a subset of the data was created including only observations made in the first two days of shelters that had a single *D. antillarum* at the start of the night. The difference in number of *D. antillarum* between the start of the night and the next morning was modelled with GLMMs using the glmer function in the R package "lme4". A binomial distribution was used (family=binomial) as the difference in *D. antillarum* at the beginning and end of the night was either 0 or 1 (presence-absence data). Treatment and total number of interactions were considered as fixed factors. To account for dependency, the same shelter was surveyed multiple nights, shelter ID was included as a random factor. Model selection was performed based on AIC (Zuur et al., 2009, Bolker et al., 2009). For statistical inference, likelihood ratio tests (LRT) were performed using the drop1 function (Zuur et al. 2009).

All statistical analyses were performed with R (R Core Team, 2021) using R studio version 1.2.5001. P-values <0.05 were considered statistically significant. Reported values are mean ± standard deviation, unless otherwise indicated. The R package "ggplot2" was used to construct the graph.

Results

Retention of *D. antillarum* on the artificial reefs was significantly affected by caging (LRT = 13.41, df = 3, P < 0.001) and day of the experiment (LRT = 56.17, df = 1, P < 0.001), the latter having a strong negative affect on retention. Retention was not significantly affected by source of the sea urchins. Artificial reefs with uncaged wild and lab-reared *D. antillarum* had respectively 21 ± 47 % and 25 ± 29 % average survival of restocked *D. antillarum* (Fig. 5). Of the controls, all caged wild and seven out of eight lab-reared caged *D. antillarum* survived the experiment.

Picture analysis resulted in 648 coded sightings. All of those included *D. antillarum* predators and no sightings were recorded of *D. antillarum* outside their shelter without a predator present (code 8 and 9). Of all predator sightings (Table 2), 189 included a predator more than 50 cm from an artificial reef module (code 1). 293 sightings included predators within 50 cm but not closer than 10 cm of an artificial reef (code 2), 40 sightings included predators within 10 cm of an artificial reef (code 3) and 136 sightings include interactions between the predator and *D. antillarum* (code 4). There was a single sighting of a *D. antillarum* outside its shelter, on the sand, with a predator within 50 cm (code 5) and another single sighting of a predator attacking that same individual (code 6). No sightings were observed of a predator feeding on *D. antillarum* (code 7). The queen triggerfish *B. vetula* was by far the most abundant predator with 589 sightings, followed by the porcupinefish *D. hysterix* with 23 sightings and the Caribbean spiny lobster *P. argus*, which was sighted 22 times. Of all predators, only *B. vetula* and *B. rufus* approached the reef within 10 cm of the shelter of the reef (code 3 and 4). For *B. rufus* this was recorded twice, while the other 176 sightings concerned *B. vetula*. Most of these sightings (135) concerned interactions between *B. vetula* and *D. antillarum*. Over the course of the experiment, *B. vetula* was observed 6.0 ± 4.1 times within 10 cm of a shelter on an artificial reef restocked with wild *D. antillarum*. This was not significantly different compared to reefs restocked with lab-reared *D. antillarum*, where *B. vetula* was seen 3.8 ± 2.2 times within 10 cm of a shelter. Interactions of *B. vetula* with *D. antillarum* were observed significantly more often on reefs restocked with wild compared to lab-reared *D. antillarum* (LRT = 11.72, df = 1, P < 0.001). Per artificial reef, 26.2 ± 15.8 interactions were observed between *B. vetula* and wild *D. antillarum*, while 7.5 ± 2.7 interactions were observed between *B. vetula* and lab-reared *D. antillarum*.

Total number of interactions during the day on a certain shelter had a significant effect on the retention of *D. antillarum* in that shelter during the following night (LRT = 8.36, df = 1, P = 0.004). For shelters that retained a *D. antillarum* at the end of the night (n=34), 0.93 ± 1.52 interactions with predators were recorded during the previous day. For shelters that lost their *D. antillarum* during the night (n=22), 3.48 ± 6.20 interactions with predators were recorded. Treatment had no significant effect on the retention and was not included in the best fitting model.

A total of six *D. antillarum* predator species were sighted during the roving diver survey. The Caesar grunt *H. carbonarium* was the most abundant with four sightings, followed by two

sightings of the spotted spiny lobster *P. guttatus.* The black margate *A. surinamensis*, Caribbean spiny lobster *P. argus,* queen triggerfish *B. vetula* and Spanish hogfish *B. rufus* were all sighted once.

Discussion

Retention of *D. antillarum* on the artificial reefs was relatively low with 25-30 % after 10 days. This was expected, as the current study is a follow-up on a restocking attempt at a nearby location, where a restocking experiment resulted in a mean retention of 60% after 2 months and 0% after 3 months (de Breuyn, 2021). The sharp decline in *D. antillarum* in less than two weeks in the current study makes it unlikely that any of the restocked individuals would have remained on the artificial reefs for longer than a few months. Caged lab-reared and wild *D. antillarum* survived for the full duration of the experiment, indicating that potential stressors related to the transportation (*e.g.* changes in oxygen, salinity, and temperature) or handling of *D. antillarum* seem to be of minor concern and other factors negatively affected retention. Retention of restocked *D. antillarum* is thought to be mediated by predation pressure, habitat, food availability, and behavioural tendencies (Miller et al 2007; Keller and Donahue, 2006; Williams 2022).

Based on the removal of *D. antillarum* within hours after restocking during a previous experiment (de Breuyn, 2021) we hypothesized that diurnal predation would be the major factor affecting retention. Contrary to this hypothesis, no *D. antillarum* predation was recorded in this study. We did, however, observe many predator-prey interactions, of which the majority was conducted by *B. vetula*, which is known as one of the most important predators of *D. antillarum* (Randall et al., 1964). Next to *B. vetula,* many other fishes and crustaceans are known as predators of *D. antillarum* (Randall et al. 1964; Kintzing and Butler, 2014). Of those, *D. hysterix, B. rufus* and *P. argus* were regularly observed on the remote photos. Only *B. rufus* was observed two times close to the shelter entrance and one of these sightings concerned an interaction. In addition to the predators recorded on photo, *A. surinamensis, H. carbonarium* and *P. guttatus* were recorded on the adjacent reefs during a roving diver survey. Apparently, most of the predators observed on photos and during the roving diver survey, were not attracted by the presence of *D. antillarum*. This may be an effect of the continued low local densities of *D. antillarum*, which could have resulted in dietary shifts of certain predators (Reinthal et al., 1984). The reefs surrounding the experimental site had very low *D antillarum* densities with no individuals observed during this study (personal observation of all authors) and we assume *D. antillarum* do not form a significant dietary proportion of predators in the area. More generalist predators such as the wrasses and grunts could therefore be less attracted by low densities of *D. antillarum*. More specialized predators, such as *B. vetula* were able to persist after the 1983-1984 *D. antillarum* die-off by switching to other prey items in the absence of their primary prey

(Reinthal et al., 1984), but might still prefer *D. antillarum*. Limited observations of other predators could also be explained by aggressive territorial behaviour of *B. vetula* (Sevon, 2020). Male queen triggerfish establish harems of several females and are known to aggressively defend their territories, especially their nests, during the spawning season (Bester, 2017). The spawning season of *B. vetula* is between December and August and includes multiple spawning events per season (Rivera Hernández et al., 2018). As the present study took place in April, there is a high chance of it falling within *B. vetula* spawning season.

The low success of predation attempts indicates that the shelter of the Moreef modules provided suitable protection for *D. antillarum* during the day. The remote photos of the interactions indicate that the shelters were too narrow for the snout of *B. vetula* to reach *D. antillarum* at the deep end of the crevice. Dame (2008) conducted a restocking experiment with *D. antillarum* around Curaçao and already concluded that the shape of the shelter affects retention. Both types of shelter tested by Dame (2008) showed a decrease in retention throughout the 3-week observation period, but the persistence of *D. antillarum* was significantly higher in "tunnel" shelters than in "hut" shelters, which had 0% retention after 16 days. Although the shelters of the artificial reefs used in the present study provided protection during the day, the predator-prey interactions still appeared to affect *D. antillarum* retention, as shelters that were attacked often during the day had a higher chance of being vacated the following day. Thus, the depth of the artificial reef shelters (20 cm) was not deep enough to prevent predator-prey interaction altogether and day-time attacks likely resulted in nocturnal migration off the artificial reefs. Carpenter (1984) showed that *D. antillarum* can assess the quality of their shelter and that poorer quality crevices were more readily vacated after simulated predation, something that also could have happened during the present study. Other restocking studies have hypothesized that habitat features were a driver of losses in retention (Miller et al., 2007; Keller and Donahue, 2006). Small test reefs (Miller et al., 2007; Levitan and Genovese, 1989) and limited reef complexity (Keller and Donahue, 2006; Dame, 2008) were possible explanations for migration, which coupled with the high predation pressure on some individuals could have expedited nocturnal migration in the present study. Another incentive for migration is to find conspecifics to aggregate with. This is a known defence mechanism of *D. antillarum* (Kintzing and Butler, 2014) and has been experimentally shown to increase juvenile survival (Miller et al., 2007). The limited size of the artificial reefs used in this study did not allow large *D. antillarum* aggregations and could have been a reason for migration off the artificial reef.

Contrary to our hypothesis, wild *D. antillarum* were attacked significantly more often compared to lab-reared individuals. This was unexpected, as lab-reared *D. antillarum* can exhibit reduced sheltering behaviour, which would increase vulnerability to predation, compared to wild urchins (Sharp et al. 2018). Nonetheless, in our study, no *D. antillarum* were recorded outside their shelter, as both lab-reared and wild *D. antillarum* were sheltering towards the back of the shelters. It could be that our urchins were more accustomed to a normal day-night rhythm,

something that was also observed by Hassan et al. (2022). In addition, the high number of unsuccessful daytime attacks likely provided increased stimulus for the diel sheltering patterns observed (Carpenter, 1984). A final explanation for the higher number of interactions on wild *D. antillarum* is that they were slightly bigger compared to the lab-reared urchins. Possibly, *B. vetula* prefers larger prey or it could be that larger prey is simply more readily detected or easier to attack, as they can retract less far in the shelter. The higher number of interactions on wild *D. antillarum* did not affect the final retention, which was similar for both sources.

The effect of interactions during the day on the chance a shelter is vacated during the night reduces the possibility that shelters were vacated by *D. antillarum* searching for food elsewhere. Although this alternative hypothesis cannot be totally disregarded, the artificial reefs were well overgrown with turf algae and some macroalgae, which reduces the chance that *D. antillarum* were wandering off in search of food. Nevertheless, causation of post-translocation movements remains poorly understood and attempts to stock reefs with higher densities of adults (Wynne, 2008) and on high rugosity reefs (Keller and Donahue, 2006) still resulted in migration, even if predation remained low. Williams (2022) notes that translocated urchins will disperse freely and need to be corralled for experimental manipulations, indicating unknown factors influence retention. Although not part of our study design, we opportunistically inspected the surrounding reefs for *D. antillarum* during this study. Like Miller et al. (2007) and contrary to Dame (2008) and Williams (2022), not a single *D. antillarum* was found, suggesting that migration, if it occurred, was disrupted by predation during the night. Individual *D. antillarum* on sand have little protection (Levitan and Genovese, 1989), which could be an explanation why these individuals were not found back. Additionally, some *D. antillarum* may have been attacked when they were still residing on or in the artificial reef modules during the night. Of the predators that were present on the surrounding reefs, *D. Hystrix* (Carpenter, 1984), *P. argus* (Lozano-Alvarez and Spanier, 1997), *P. guttatus* (Kintzing and Butler, 2014) and *A. surinamensis* (McClanahan, 1999) are known to be nocturnal.

Conclusions

We conclude that the low retention of *D. antillarum* during the present study is likely a result of predation or migration at night. The deep shelters of the artificial reefs used in this study prevented successful predation but did not prevent interaction between predators and *D. antillarum*. Unsuccessful attacks by *B. vetula* during the day likely resulted in migration away from the artificial reef during the night, possibly followed by predation when the *D. antillarum* were vulnerable on sand. No indications were found that lab-reared individuals were less suitable than wild *D. antillarum* for restocking practices, although it cannot be ruled out that lab-reared individuals were initially attacked less because of their smaller size. To increase restocking success, future restocking attempts should be conducted on artificial or natural reefs that have

shelters more than 20 cm deep, so *D. antillarum* can retract far enough to avoid predator-prey interaction. We recommend monitoring restocked *D. antillarum* also at night and at other locations, to determine the causative factors for low *D. antillarum* retention, including identification of the most important predators. This information is essential to give coral reef managers the opportunity to increase *D. antillarum* restocking success by selecting reefs with a lower predator density, giving restocked *D. antillarum* an acclimatization period in a protected environment (Williams 2022), and/or conduct temporary predator control measures. Since Caribbean coral reefs continue to degrade and a new die-off reduced *D. antillarum* densities in large parts of the Caribbean in 2022 (Hylkema et al., 2023), the development of effective restocking practices is urgently needed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure 1

Location of Saba in the Caribbean.

Location of Saba in the Caribbean. Experiments were performed at Big Rock Market and wild *Diadema antillarum* were collected at Diadema City.

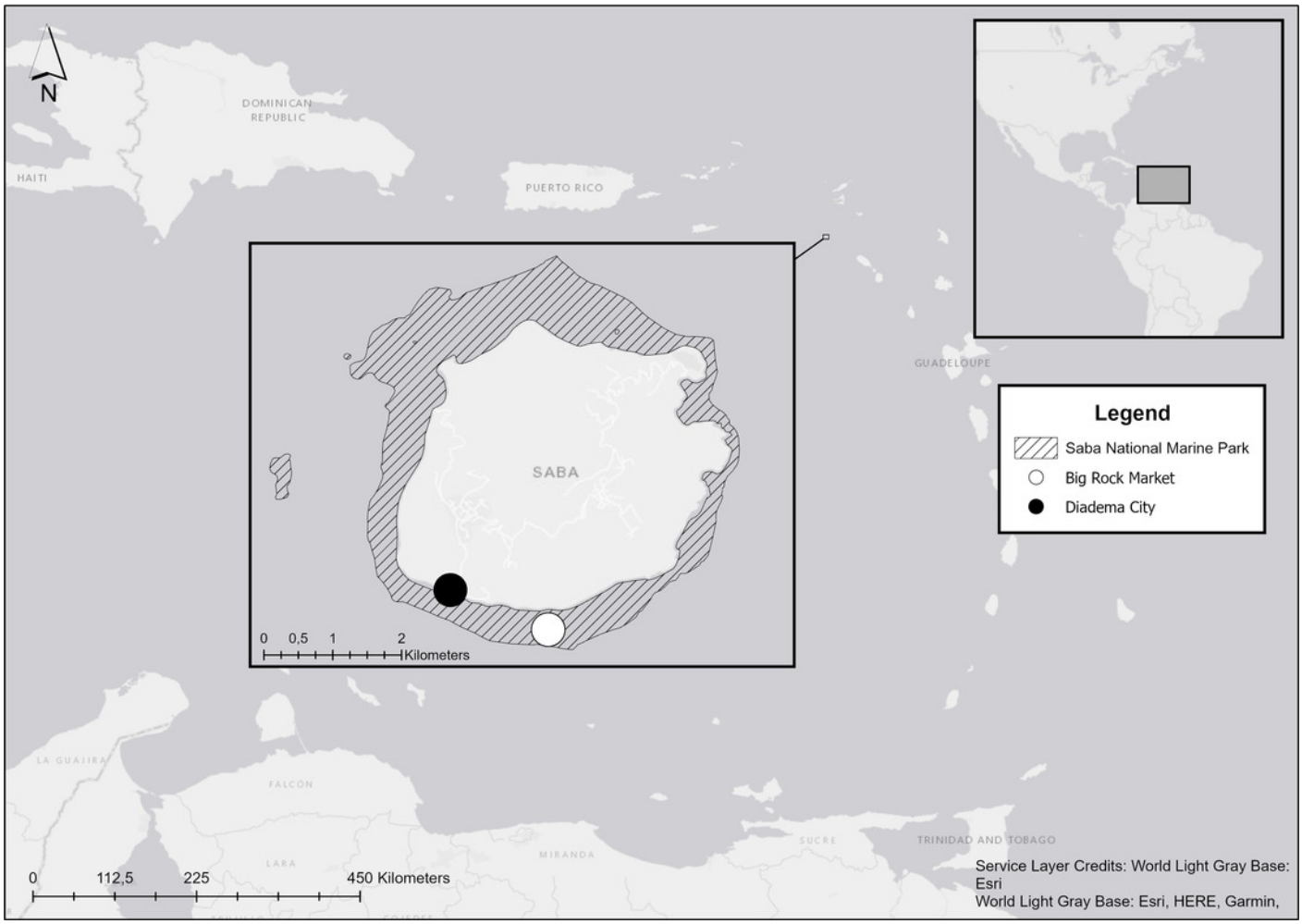
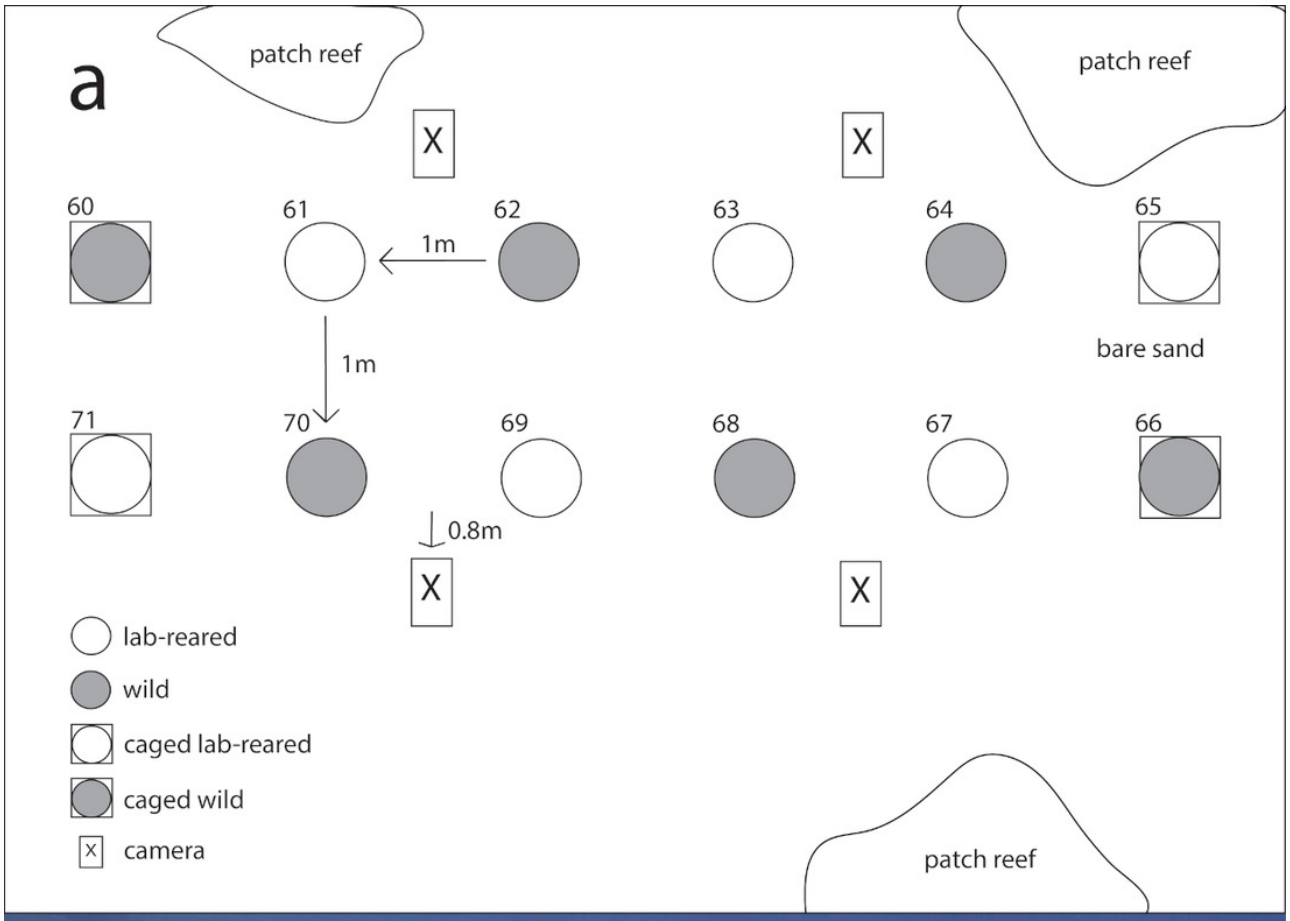


Figure 2

Experimental setup.

(a) Schematic overview of the experimental setup. (b) Photo of the experimental setup.


a
patch reef
patch reef
X
X
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61
62
63
64
65
1m
1m
bare sand
71
70
69
68
67
66
0.8m
X
X
lab-reared
wild
caged lab-reared
caged wild
camera
patch reef


b

Figure 3

Moreef artificial reef module.

Front view of Modular Restoration Reef (Moreef) module with incorporated shelters.

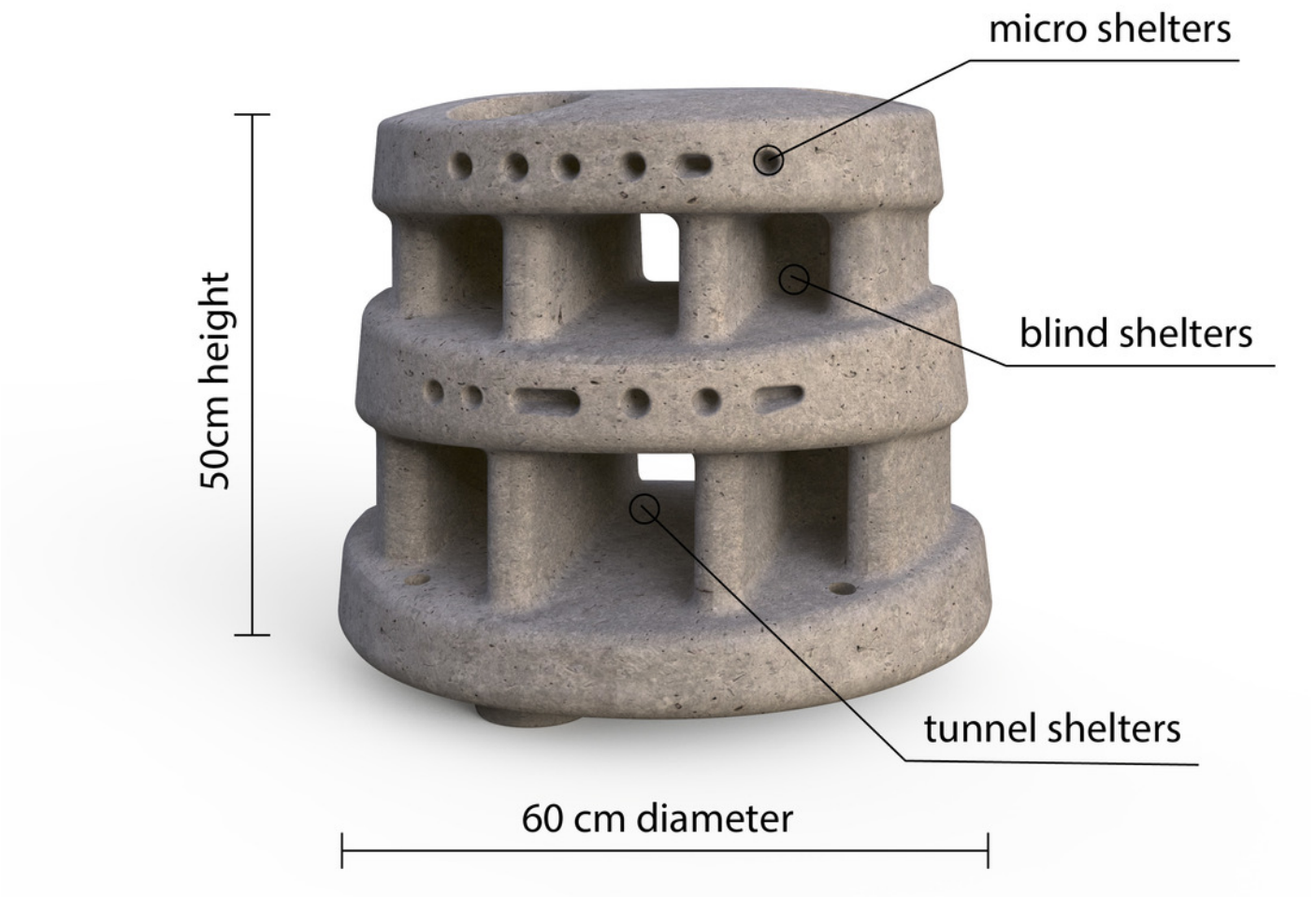

Figure 4

Codes to categorize actions of predators and *Diadema antillarum*.

Codes used in this study to categorize actions of predators and *Diadema antillarum*: (a) Code 1: *D. antillarum* predator is present outside of a 50 cm virtual sphere around the artificial reef. (b) Code 2: *D. antillarum* predator is present within a 50 cm virtual sphere around the artificial reef, but not within 10 cm radius around the shelter entrance. (c) *D. antillarum* predator is present within 10 cm around the shelter entrance of the artificial reef. (d) Code 4: Interaction between *D. antillarum* predator and *D. antillarum* on the artificial reef. (e) *D. antillarum* predator is present within a 50 cm virtual cylinder around *D. antillarum* which is located outside the shelter. (f) *D. antillarum* predator attacks *D. antillarum* which is located outside the shelter.

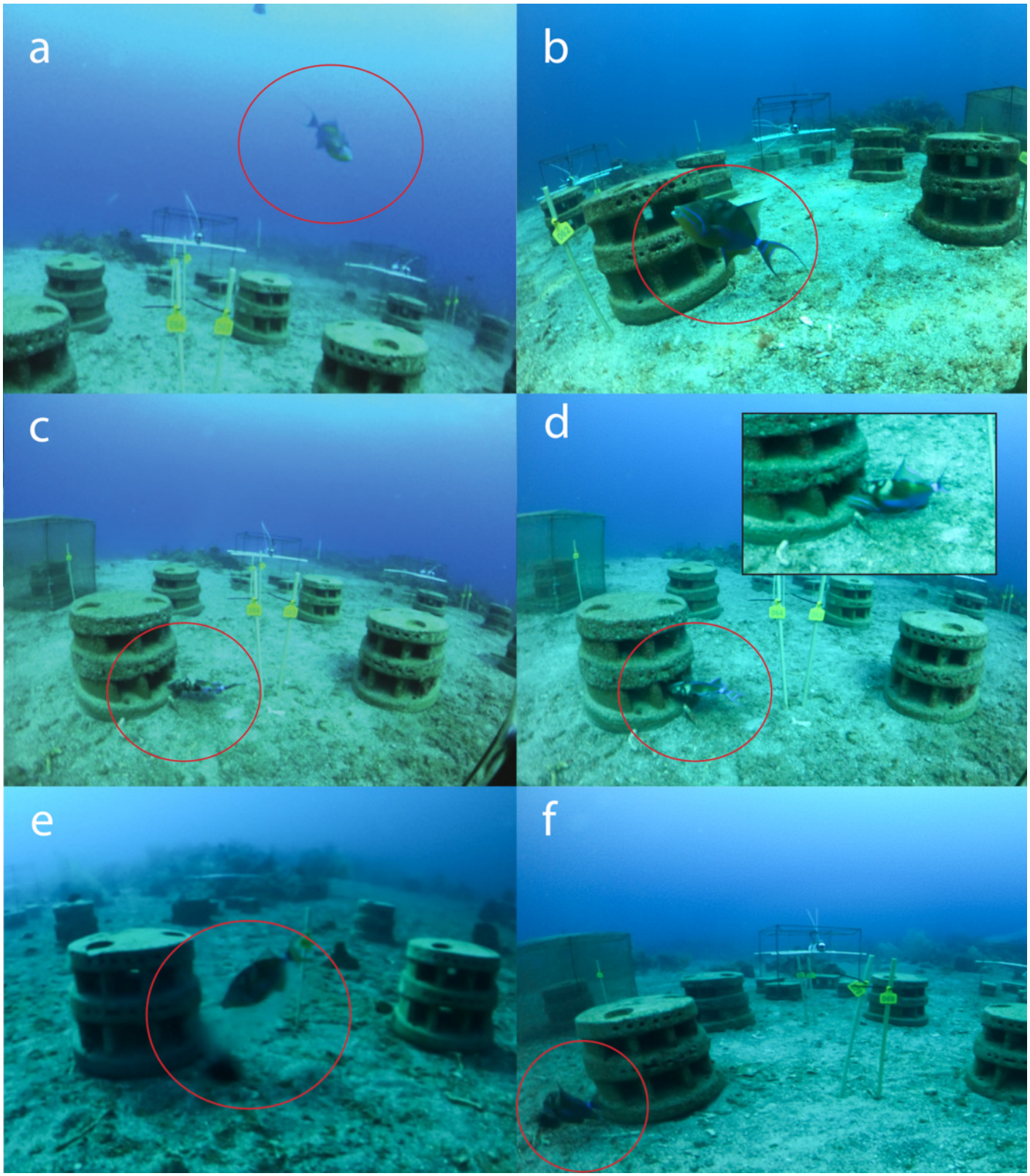
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Figure 5

Diadema antillarum retention

Average *Diadema antillarum* retention (± SE) per treatment on artificial reefs over time.

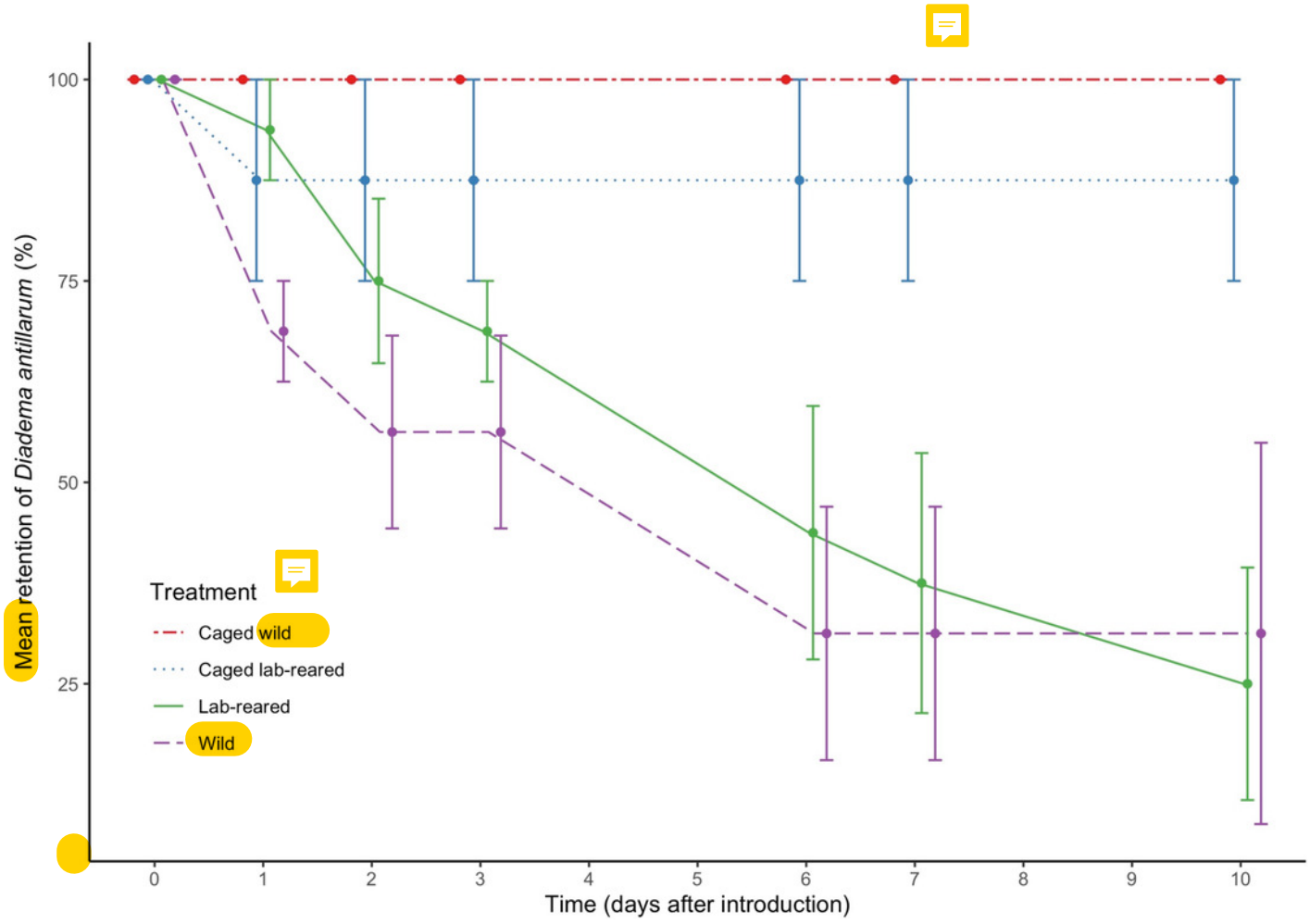

Table 1(on next page)

Codes for sightings and predator-prey interactions.

Codes for sightings and predator-prey interactions. Pictures were only attributed to the most precise code describing the action. Code examples shown in Figure 4.

Code	Definition
1	*D. antillarum* predator is present outside of a 50 cm virtual sphere around the artificial reef.
2	*D. antillarum* predator is present within a 50 cm virtual sphere around the artificial reef, but not within 10 cm radius around the shelter entrance.
3	*D. antillarum* predator is present within 10 cm around the shelter entrance of the artificial reef.
4	Interaction between *D. antillarum* predator and *D. antillarum* on the artificial reef.
5	*D. antillarum* predator is present within a 50 cm virtual cylinder around *D. antillarum* which is located outside the shelter.
6	*D. antillarum* predator attacks *D. antillarum* which is located outside the shelter.
7	*D. antillarum* predator feeds on *D. antillarum* outside the shelter.
8	*D. antillarum* is outside the shelter and present within a 50 cm radius around the artificial reef. No *D. antillarum* predator present.
9	*D. antillarum* is outside the shelter and present outside of a 50 cm radius around the artificial reef. No *D. antillarum* predator present.

1

Table 2 (on next page)

Diadema antillarum predator sightings

Overview of all *Diadema antillarum* predator sightings (n) categorized per code per predator species and in total. Predator species are sorted based on their number of sightings.

Common name	Scientific name	Potential predator > 50cm of artificial reef	Potential predator < 50cm of artificial reef	Potential predator < 10cm of artificial reef	Interaction predator and *D. antillarum*	Potential predator <50 cm of *D. antillarum* outside shelter	Potential predator attacks *D. antillarum* outside shelter	Potential predator feeds on *D. antillarum*	Total actions per species:
	Code	**1**	**2**	**3**	**4**	**5**	**6**	**7**	
queen triggerfish	*Balistes vetula*	159	254	39	135	1	1	0	**589**
porcupine fish	*Diodon hysterix*	20	3	0	0	0	0	0	**23**
Caribbean spiny lobster	*Panulirus argus*	7	15	0	0	0	0	0	**22**
Spanish hogfish	*Bodianus rufus*	0	9	1	1	0	0	0	**11**
bandtail pufferfish	*Sphoeroides spengleri*	2	0	0	0	0	0	0	**2**
saucereye porgy	*Calamus calamus*	1	0	0	0	0	0	0	**1**
Total actions per code:		**190**	**281**	**40**	**136**	**1**	**1**	**0**	**648**

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