Radboud University, Faculty of Science
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Comparing the health and growth of newly transplanted staghorn corals on four different outplant sites

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Contents

1. Abstract

Coral reef ecosystems are important on a global level because of their function in the marine ecosystem and their economic value to humans. However, they have been greatly impacted by human influence in the past few decades, mainly because of climate change. Coral reef cover has declined by almost 80% in the Caribbean, and on Curacao the two most common *Acropora* species have declined by 98%. Coral restoration is one of the methods used to counteract this impact, and it is important to take into account ecosystem interactions when designing coral restoration projects. In this research, the effectiveness of asexual coral restoration methods using *Acropora cervicornis* on Curaçao was examined, specifically the placement of the outplant sites. To assess the effectiveness of the methods used, the coral fragments themselves were assessed, as well as several biotic and abiotic factors. The main focus of the research was to determine which of the biotic and abiotic factors could explain the variation in coral growth and health. The sites showed clear differences in temperature and light, but not in nutrient concentrations and sedimentation. Additionally, differences were found between sites when looking at coral colour, but no differences were found when looking at coral growth. The main factors predicting coral colour were sedimentation, algae cover, biodiversity index, total biomass and the herbivore proportion of the biomass. The factors predicting coral growth were sedimentation rate and biodiversity index. As for biotic factors, differences were found in biodiversity index, weighted mean of the biomass and algae cover. The majority of the results were not in line with the hypothesis. This is possibly due to irregularities in the data sampling methods, mainly in the frequency of the measurements. Another option could be that the sites are not measurably different because most of the sites were situated in the same bay. More research is needed to be able to make clear conclusions. What can be concluded is that there are differences between the sites when looking at coral health and environmental factors, and that the coral growth and survival rate were high on all sites. This is important information for future coral restoration efforts.

1.1 Keywords

Coral restoration, Curaçao, Caribbean, *Acropora cervicornis*, Seagrass, Coral nursery

2. Introduction

2.1 Coral reef ecosystems

Coral reefs are an important coastal habitat. Coral reefs play an important role in underwater habitats by functioning as nurseries for around 32% of all marine species. Other than that, reefs provide coastal protection by breaking large waves and tsunamis. Additionally, coral reefs also play an important role for human society. Globally, at least 6 million people fish on coral reefs. Additionally, reef-related tourism is an important source of income for coastal regions. The global economic value of coral reefs has been estimated to around 10 trillion US dollars per year (Knowlton et al. 2021).

Coral reefs consist of many coral colonies of different species. A coral colony is made up of many small coral polyps that communicate and work together to form a large coral. These polyps belong to the order of Cnidaria and are related to jellyfish. They engage in a symbiotic relationship with unicellular algae called zooxanthellae, where the algae provide food through photosynthesis, and the coral polyp provides protection (Muller-Parker et al. 2015; Pearse and Muscatine 1971; Yamashita et al. 2014). The coral species addressed in this research is *Acropora cervicornis* (Lamarck, 1816), also known as staghorn coral. Staghorn coral is a reef-building coral forming large branching thickets (Fig. 1).

Figure 1 A large thicket of staghorn coral (A. cervicornis) on Bonaire, Dutch Caribbean. Photographer: Jente van Langerak.

Coral reefs are built by reef-building corals, which are fast-growing hard corals. These corals create large structures that are the basis of coral reef habitats (Putnam et al. 2017). The traits and life history of coral species influence the structural complexity, defined as the

physical three-dimensional configuration of a reef. A change in the coral species composition therefore can lead to changes in the structural complexity of a reef (Darling et al. 2017). A higher structural complexity of coral reef ecosystems increases fish diversity, abundance, and biomass (Darling et al. 2017; Graham and Nash 2013). The formation of reefs, and therefore also their structural complexity, is impacted by humans (Williams et al. 2019). Through human-caused disturbance effects (see paragraph 2.2), shifts take place in the dominant species within a coral ecosystem, and the proportions of coral species change, thus changing the structural complexity (Bellwood et al. 2019; Inoue et al. 2013). Humans have greatly impacted coral reefs over the past few decades (Williams et al. 2019).

2.2 Dangers to coral reefs

Because coral reefs are so important, their status is of global concern. Coral reefs are being heavily impacted by climate change and other human influences.

Globally, coral reef cover has declined almost 14% percent in the last 20 years (Souter et al. 2020). In the Caribbean alone, coral cover has declined by almost 80% since the 1970s. When looking at *Acropora* species, specifically *A. cervicornis* and *Acropora palmata* (Lamarck, 1816), the occurrence of these two species has declined by 98% on Curaçao in the last four decades (GMN 2020). The main reason for this is global warming, which leads to rising ocean temperatures and ocean acidification (Knowlton et al. 2021). Heat stress has a significant impact on the zooxanthellae and pigments in corals (Schoepf et al. 2021). Additionally, climate change leads to high mortality and low larval recruitment in corals. Some species, like *Acropora*, are affected more but also recover faster, while other coral species are more resilient but when they are damaged take a long time to recover (Bellwood et al. 2019). This seems to be partly due to their growth rate, as *Acropora* are fast-growing (Renema et al. 2016).

This decline in coral cover caused a massive change in the communities surrounding these reefs (Aronson and Precht 2001; Jackson et al. 2014; Rafe et al. 2005; WAITT 2017). A shift to other species, like algae, has been observed (Bellwood et al. 2019), though this might in part be slowed down by a shift in the fish species in terms of feeding guilds. For example, when an increase of algae takes place due to a disturbance, this is usually followed by an increase of herbivores, as there is more food availability (Wilson et al. 2009). The feeding habits of these fish can then slow down the shift to algal dominance. However, the fish community is also impacted by overfishing, so a changing fish community can cause an increase of algae if herbivores are being overexploited. Therefore, it is important to take feeding guilds into account when assessing the fish community. Examples of disturbances other than climate change are trawling, dropping anchors and infrastructure development, all of which cause structural damage to reefs (Knowlton et al. 2021). Increased terrestrial runoff due to urbanization (Müller et al. 2020) also increases sedimentation in coastal regions, which impacts corals negatively (Fabricius 2005). Additionally, inflow of nutrients via wastewater leads to algae blooms and more coral diseases (Knowlton et al. 2021), which might also impact the shift from coral-dominated ecosystems to algae-dominated ecosystems. Once this shift has taken place, it is harder for corals to re-establish themselves (Diaz-Pulido et al. 2010).

2.3 Coral reef management

To preserve the remaining coral reef ecosystems, urgent action is necessary. One of the methods currently in use to counteract damage to coral reefs is coral restoration. There are multiple methods of coral restoration, but the two main directions it can take are sexually and asexually, based on the two different reproduction methods of corals (outlined in Fig. 2).

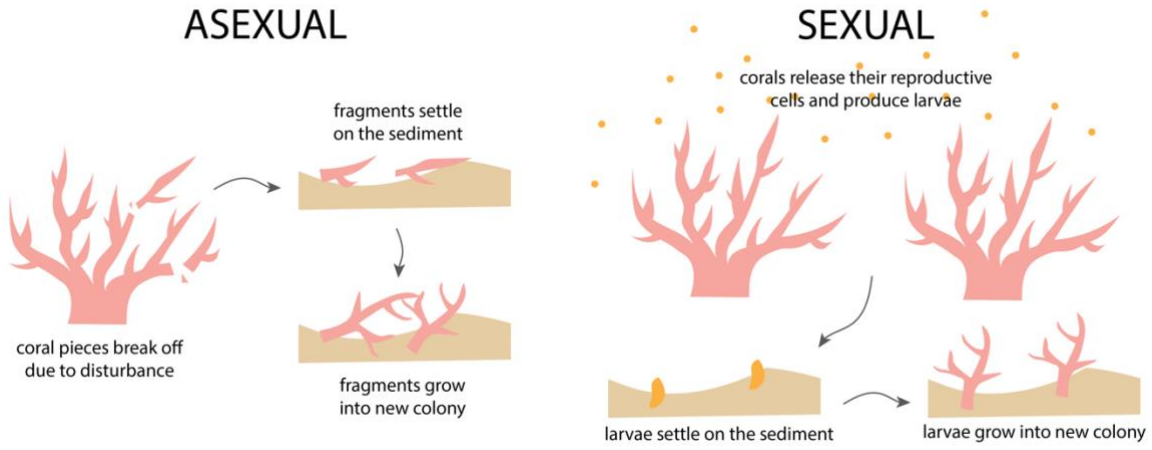

Figure 2 Asexual and sexual coral reproduction. Figure created by Jente van Langerak.

Sexual coral reproduction consists of coral spawning, where several times a year all the individuals of the same species release their gametes into the ocean. If fertilisation is successful, these gametes will develop into coral larvae which will actively search for a suitable substrate on the reef to settle down and form a new sessile coral polyp (Fadlallah 1983). Sexual coral restoration is done through collecting gametes after a coral spawning event and raising these in a laboratory. Once they have settled on substrates and metamorphosed into juvenile coral recruits, they can be transplanted onto the reef (Chamberland et al. 2015). About a decade ago, sexual production of *A. cervicornis* colonies had so strongly declined on Curaçao, making asexual methods seem the only way to productively reproduce staghorn corals (Vermeij et al. 2011). However, in more recent years coral spawning has improved again due to restoration efforts (pers. comm. M. van Aalst, 2023). This method of coral restoration has the benefit of maintaining the genetic diversity of a coral population, as new individuals are formed with their own unique genotype (Baums et al. 2013). However, it is dependent on coral spawning events, which only happen a few times a year. Additionally, the coral larvae are very fragile, and many of them do not survive long-term (Chamberland et al. 2015).

Asexual coral reproduction occurs through fragmentation, meaning that part of a coral breaks off the colony and will form a new colony dislocated from the original coral colony. The specifics of the asexual method of restoration are outlined in paragraph 2.4. The benefits of this method of coral restoration, also called “coral gardening”, are mostly due to its accessibility. Fragmentation of corals can happen at any time during the year, and because the fragments are already larger in size than larvae, their survival rate is much

higher (Johnson et al. 2011). Therefore, results are much more imminent. However, this method does not increase the genetic diversity, and care has to be taken during the process in order to maintain the genetic diversity and not decrease it. This is done by for example taking fragments from different pieces of a reef instead of just one singular location (Baums 2008). Corals with identical genotypes will not reproduce sexually (Johnson et al. 2011), so taking fragments from different colonies ensures that sexual reproduction could be possible in the future. Due to its accessibility and the wide use of this method on Curacao, this research will use asexual coral restoration methods.

Though coral restoration efforts can be very effective in increasing coral cover, they do not actually address the root cause. Coral reef restoration can improve reef resilience in the long term, but according to Hein (2020), the focus should be more on maximizing coral species richness, and not just restoring endangered species. What is important to note, though, is that site selection is important for maximizing restoration outcomes, and a large scale should be considered, taking into account ecosystem processes. More knowledge on ecosystem interactions could lead to better conservation efforts (Bellwood et al. 2019). In the Caribbean, the main focus is on restoring *Acropora* species, but only planting these species seems to lead to more disease and predators in the planted areas. Maximizing the diversity of the transplants in terms of coral species might help against these processes (Hein et al. 2020). In any case, any restoration efforts should be coupled with global carbon reductions as well as other human impacts to address the symptoms as well as the cause (Bellwood et al. 2019). A multidisciplinary approach seems to be the most effective (Knowlton et al. 2021).

2.4 Coral restoration on Curaçao

On Curaçao, where this research was executed, strict guidelines are in place regarding coral restoration. These guidelines are regulated by the Agriculture and Fisheries Department of the Ministry of Health, Environment and Nature of Curaçao (GMN). Any organization that is planning on starting a coral restoration project has to go through an application process to make sure they adhere to the guidelines. In short, the guidelines state the following: The only species that can be used for asexual coral restoration on Curaçao at this moment is *A. cervicornis*. Additionally, the GMN outlines a protocol for coral restoration using *A. cervicornis* (summarized in Fig. 3; (GMN 2020)).

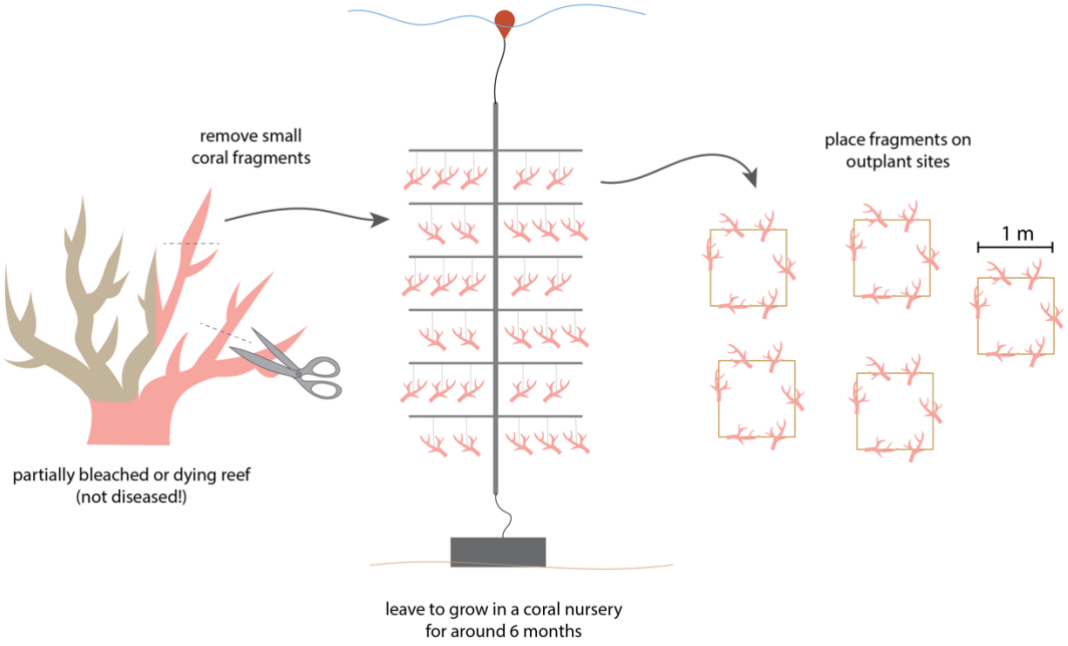

Figure 3 An overview of the coral restoration protocol used on Curaçao. Figure created by Jente van Langerak.

2.5 Ecosystem interactions

As mentioned before, ecosystem interactions could be quite important in coral reef restoration. Past research has shown that coastal ecosystems greatly influence each other. For example, mangrove forests and coral reefs, as well as seagrass meadows and coral reefs influence each other, mainly through controlling the sediment fluxes and retaining nutrients, but also through pH and temperature regulation (Camp et al. 2016; Gillis et al. 2014). Especially seagrass seems to have positive effects on coral reefs, indicating that the interaction between these two ecosystems could play an important role in coral restoration. Additionally, within an ecosystem there are important interactions between different communities that should be taken into account such as the interactions between predator and prey species (Bailey et al. 2010). Finally, terrestrial ecosystems, as well as human-made ecosystems such as cities, can have a large impact on coral reef ecosystems. For example, as mentioned before, increased urbanization and human behaviour in cities has drastically increased runoff of pollutants from cities into the ocean (Müller et al. 2020), .

The presence of seagrass significantly decreases the abundance of bacterial pathogens that may cause infections in humans and marine organisms (Lamb et al. 2017). Moreover, Gillis et al. (2014) showed that the presence of seagrass results in lower waves, higher nutrient levels and higher algivore abundance. Another important function of seagrass meadows is the trapping of sediment, which also benefits coral reefs (Gillis et al. 2014) When confronted with rising sea temperatures, the presence of seagrass also seems to help stabilize the coral's metabolism, heightening their calcification rate and slowing the growth of macroalgae (Liu et al. 2020). This is consistent with the findings of Purvaja et al. (Purvaja et al. 2018) who showed that the presence of seagrass increased the calcification of corals, as well as increased water quality because of sediment trapping and reducing acidification. Overall, the presence of seagrass seems to be beneficial to corals' health. In this research the seagrass cover will be taken into account.

There are different ways of assessing the status of a coral reef. Coral-specific parameters such as colour, coral cover and coral diversity could be determined, but environmental parameters can also indicate important information on the corals themselves (Purvaja et al. 2018; Zunino et al. 2019). Processes in an ecosystem are very important, not just static measurements (Bellwood et al. 2019). Looking at the fish community, for example, can give clear indications on the health and complexity of a reef (Bohnsack and Bannerot 1986). When looking at parameters like these, however, the community structure should be taken into account. When looking at parameters such as species richness and fish biomass, the feeding guilds could be taken into account (Wilson et al. 2009). A higher herbivore proportion, for example, usually means the algae are experiencing a lot of grazing pressure, which most likely decreases algae cover and slows down the shift to an algae-dominant system. However, even fish that do not feed on the coral reefs themselves are impacted by coral reef decline. This is probably because fish use the coral colonies as shelter, and when coral degrades, many of these shelter spaces are filled with algae, which reduces the amount of usable shelter and increases competition (Feary et al. 2009).

Another important parameter to consider when looking at coral reefs is sedimentation. Corals, especially *Acropora digitifera* (Dana, 1846), which is related to *A. cervicornis* (Faith and Richards 2012), benefit from low sedimentation rates and low amounts of suspended matter (Golbuu et al. 2011a). Fabricius (2005) also showed that increased terrestrial runoff impacts the growth and survival of hard corals. This is especially true for juvenile corals, though these results might not be applicable to each site, as hydrodynamics differ locally (Golbuu et al. 2011a). Different locations have different underwater geomorphology, which greatly impacts the flow of sediments (Golbuu et al. 2011b). Past research has shown that light and temperature can also greatly impact corals, especially their pigmentation (Hughes et al. 2017).

2.6 Research question and hypotheses

Currently overlooked is how location plays a role in determining the growth and health of newly transplanted asexually reproduced staghorn corals. In order to answer this question, the following sub-questions need to be answered:

- Do abiotic factors differ per site?
- Do biotic factors differ per site?
- Do these differences in abiotic and biotic factors result in differences in coral growth and health (colour)?
- Does the presence of seagrass result in differences in coral growth and health (colour)?

The expectation is that there will be differences in growth and coral colour between the sites, as staghorn corals are quite sensitive to disruptions. Therefore it is expected that the corals will respond differently in different environmental situations. The main factors influencing coral growth and colouration will probably be the fish community, specifically the herbivore to carnivore proportions, as well as sedimentation. As light and temperature have been shown to greatly influence coral colour, this is also expected to explain differences in coral colour between sites. As the sites are quite close to each other, the expectation is that the nutrients and salinity will not differ significantly. Possibly, the presence of seagrass will have a slight impact on the nutrients. As coral and algae are in a constant battle for space on the reef, the expectation is that on the sites with more coral cover there will be less harmful algae.

3. Methods

3.1 Preparation of the experimental setup

Figure 4 A coral nursery tree. Photographer: Jente van Langerak.

Staghorn coral fragments were collected from loose fragments or damaged reefs and attached to a treelike structure made from aluminium, PVC pipes and monofilament lines called a coral nursery (Fig. 4)(Nedimyer et al. 2011), keeping different genotypes separate. Every two weeks the nurseries were cleaned with brushes and sponges to get rid of harmful algae to ensure optimal growth conditions for the corals. Once the fragments had grown to a linear length of at least 10 cm (GMN 2020), they were attached to bamboo structures and placed on four experimental sites. The sites were as follows: sand dominated, degraded coral reef, healthy coral reef, and a site with a sparse amount of seagrass. The first three sites were located in the same bay, close to the nursery. The seagrass site was in a bay nearby (Fig. 5). On each site, five bamboo structures were placed, and six coral fragments were attached to each structure (Figs. 6 & 7). Fragments from the same original population were placed on the same structure. After two months, the fragments on the seagrass site were moved to a site close to the sand site (Fig. 5). Because these coral fragments had to be moved by car in large buckets, they were exposed to heat stress. Thus, the corals can be grouped into four different treatments: sand, degraded reef, healthy reef, and stressed. Though the term "healthy reef" is used throughout this research, this is only a healthy reef compared to other reefs on Curaçao, and is technically a reef with a high coral cover compared to the other sites.

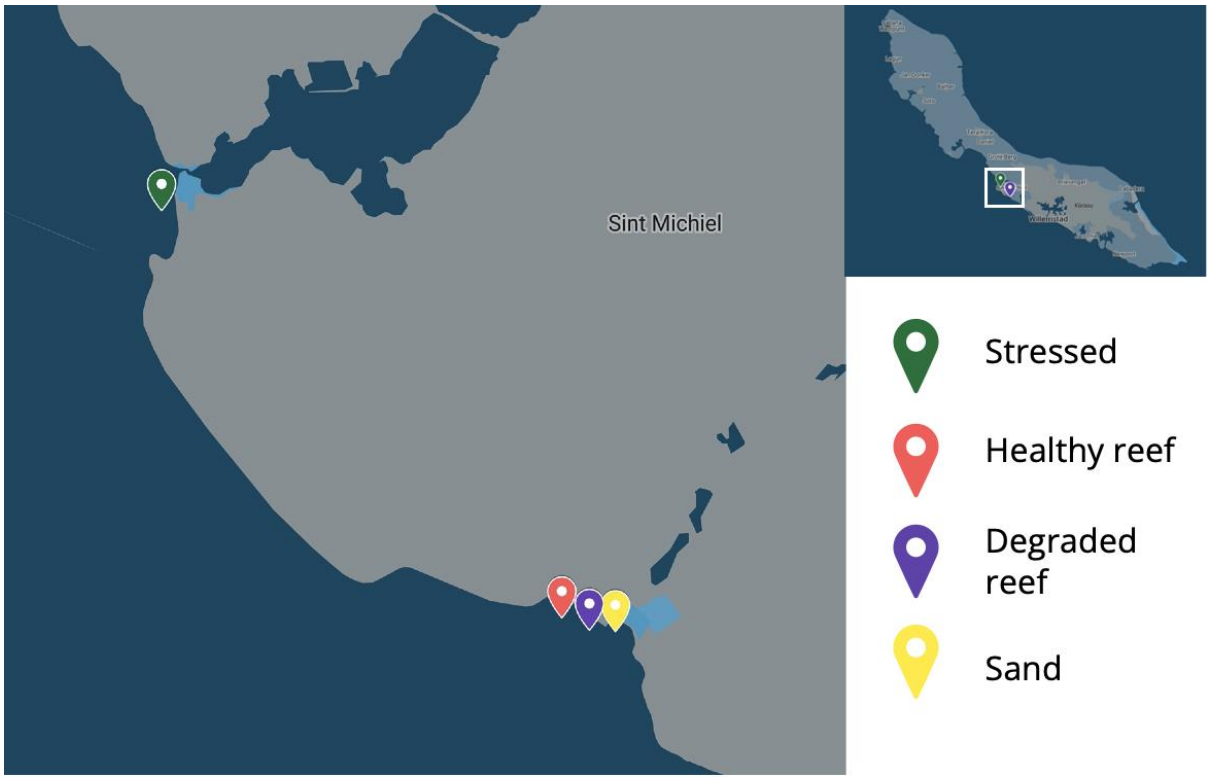

Figure 5 A map of the study sites. Figure created by Jente van Langerak using Google Maps.

Each site was also marked with metal poles placed in a circle with a diameter of 10 meters.

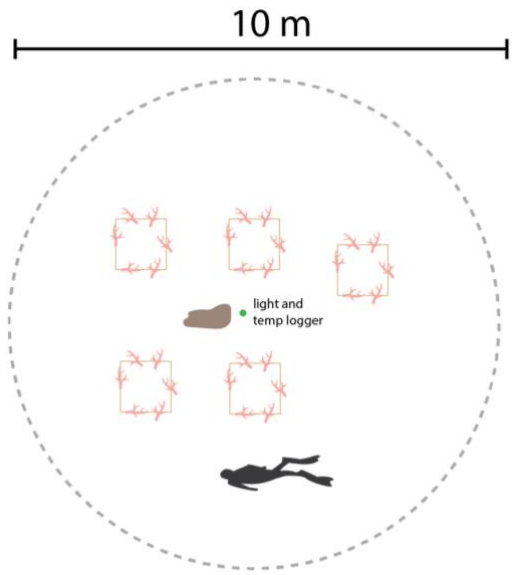

Figure 7 An overview of the study site layout. Figure created by Jente van Langerak.

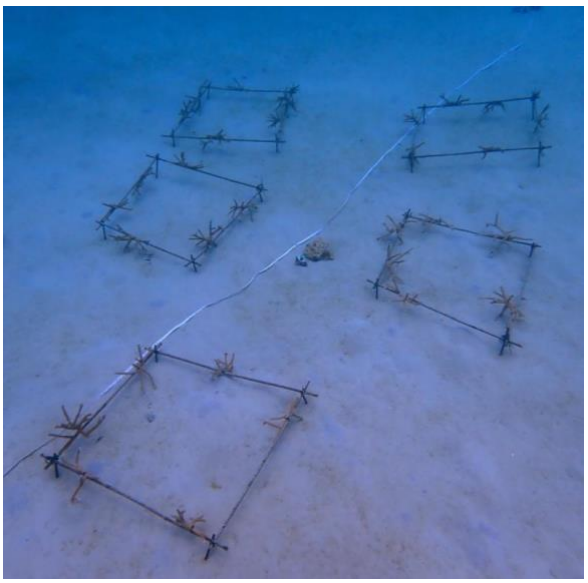

Figure 6 One of the study sites. Photographer: Jente van Langerak.

3.2 Sampling

Coral growth and colour

Over the course of three month, each month pictures of the coral fragments were taken, and their linear size and cumulative size was measured using Image J. Also, pictures of the structures were taken, and the benthic algae cover was determined using CPCe (Coral Point Count with Excel extension) (Kohler and Gill 2006). After selecting the area containing the plot and all coral fragments, 30 random points were classified into either *A. cervicornis*, sand, algae or structure (Fig. 8). CPCe then summarised those points into coverage percentages (Kohler and Gill 2006). These measurements were performed three times. Additionally, the darkest and lightest colours of the coral fragments were determined each week with a Coral Watch Health Chart (Fig. 9) on a scale from 1 to 6. The darker the coral colour, the healthier the coral (Oladi et al. 2017; Siebeck et al. 2006).

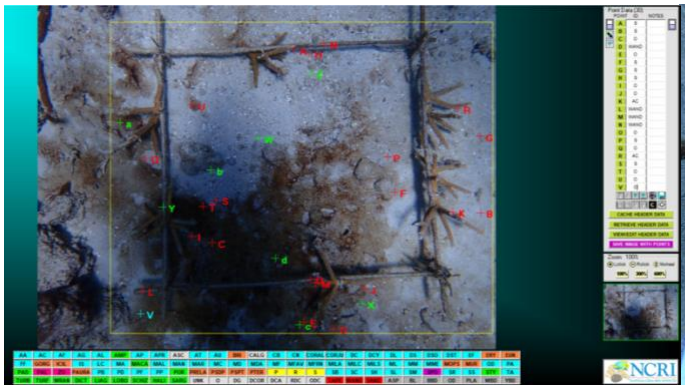

Figure 9 Classification of random points in CPCe. Photographer: Olle Juch. Figure created by Jente van Langerak.

Figure 8 Determining color with the Coral Watch Health Chart. Photographer: Jente van Langerak.

Biotic factors

Each week, a Point Count Underwater Visual Census (UVC) was executed on each study site (Bohnsack and Bannerot 1986; Samoilys 1997; Samoilys and Carlos 2000). For 5 minutes, all fish within the 10-meter circle were counted while snorkelling and marked down by species and size class, only counting the fish that were in the study area when the count started. For an additional 10 minutes, the same was done by freediving closer to the bottom to observe more benthic species. Taking into account surface time between each dive, this amounted to around 5-6 dives averaging 40-50 seconds each. Size classes used to estimate the total length of the fish were 0-10 cm, 10-20 cm, 20-30 cm and >30 cm. A comprehensive list of Caribbean fish species was studied by the researcher beforehand, so as to not lose time identifying the fish species while performing the survey.

To assess the macrobenthos population, a rock of about 40 cm diameter with sufficient holes and structure was taken from the shore and placed in-between the bamboo structures. It was left in the ocean for a month, and then taken out. Macrobenthos on the rock were determined to functional group level and their size and density was measured. This measurement was performed once.

At the seagrass site, the seagrass was quantified using a method adapted from the Seagrass Watch Protocol (McKenzie et al. 2003). The sample area was set out by laying out a cross with a transect tape of 20 m (see Fig. 10). Each five meters, a quadrant (50 x 50 cm) was placed, and the seagrass cover was determined. The length of 5 randomly selected leaves was measured to determine canopy height. This measurement was performed twice, only when the coral fragments were present.

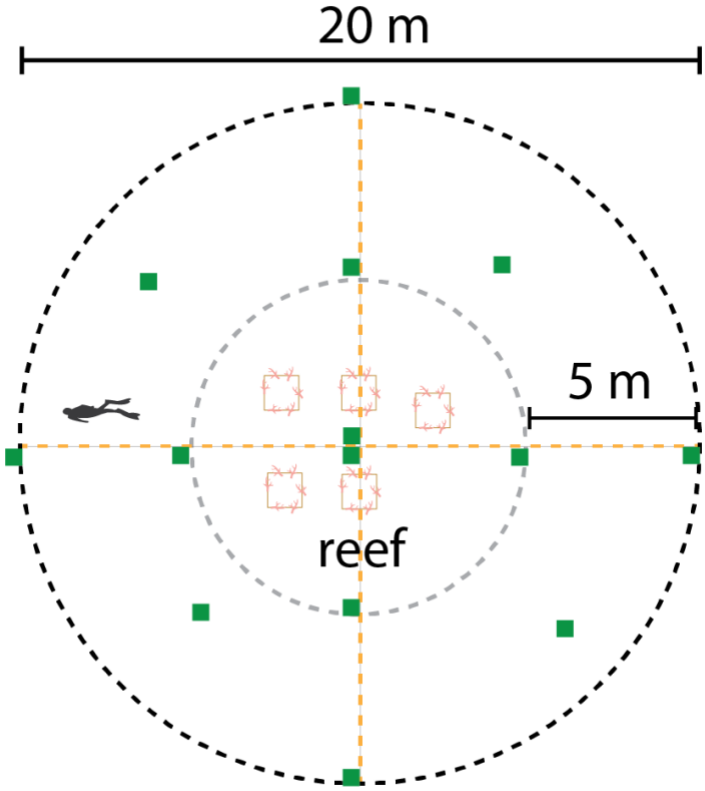

Figure 10 An overview of the seagrass sampling method. Figure created by Jente van Langerak.

Abiotic factors

Sedimentation traps were attached to the metal poles, or, when no metal pole was available, to one of the corners of the bamboo structures. The traps were kept there for 2,5 weeks and then removed. Their contents were filtered and air dried, after which the dry weight of the sediment was measured. Because the sedimentation rate was measured after the stressed corals had already been moved to another site, sedimentation traps were placed on both the old and new site.

Each month, a water sample was taken close to the sediment, in-between the structures. Using a combination of the Red Sea Marine Care Multi Test Kit, the PRO JBL Aquatest Combiset, a salinity refractometer and HACH water quality test strips, the pH, KH, NO_2, NO_3, NH_4, PO_4^{3-}, $CaCO_3$ and salinity were measured. The nutrients were measured twice. Additionally, a HOBO Light and Temperature logger (Fig. 11) was placed in the middle of the study site for the duration of the UVC. The logger measured light (in lux) and temperature (in C°) every 30 seconds. Five minutes of measurements were selected, starting five minutes after the initial placement of the logger, to allow for acclimatisation of the sensors.

Figure 11 HOBO Light and Temperature Logger in use. Photographer: Jente van Langerak.

A summary of all the measurements and their frequency is displayed in table 1.

Table 1 An overview of all the measurements

Measurement	**Frequency**	**Method**
pH, KH, NO_2, NO_3, NH_4, PO_4^{3-}, $CaCO_3$ and salinity	Monthly, twice	Red Sea Marine Care Multi Test Kit, the PRO JBL Aquatest Combiset, a salinity refractometer and HACH water quality test strips
Coral growth	Monthly	Pictures analyzed with Image J
Algae cover	Monthly	Pictures analyzed with CPCe (Coral Point Count with Excel extension)
Sedimentation rate	Once	Sedimetation containers
Macrobenthos	Once	Placement of rock that is left for a month, species on rock determined to functional group level
Seagrass quantity (only on seagrass site)	Monthly, twice	Adapted Seagrass Watch Protocol
Biodiversity index	Weekly	Underwater Visual Census

Biomass	Weekly	Underwater Visual Census
Light and temperature	Weekly	HOBO light and temperature logger
Coral color	Weekly	Coral Watch Health Chart

3.3 Statistical analysis

Calculations

From the coral size measurements, the average growth per day per fragment was calculated. From the UVC, the biomass and biodiversity were calculated.

Biodiversity was calculated with the Shannon diversity index, using the formula: $H = -\sum p_i * \ln(p_i)$, where p_i is the proportion of each species per date and site.

Biomass was calculated with the following formula: $\log(w) = \log(a) + b * \log(L)$, where w is the biomass in grams, a and b are constants specific to each species, taken from FishBase (Froese and Pauly 2023), and L is the length in cm of the specific observation. W is later multiplied by the number of observed fish (Zanke and de Froe 2015). For species where a and b values were not available, the values were taken from similar species of the same family. For the length, the average of the size class was taken; for 0-10 cm, a length of 5 cm was used, for the 10-20 cm class a length of 15 cm, for the 20-30 cm class a length of 25 cm and for the >30 cm size class a length of 35 cm. An extra column was added to the dataset, specifying the feeding guild of each species. This data was taken from data collected by Max van Aalst, and if not available there, from FishBase (Froese and Pauly 2023). The four guilds used were: herbivore, carnivore, omnivore and top predator. Community weighted means were calculated for the biomass. Additionally, the proportion of herbivore biomass within the total biomass of each site was calculated. For the coral colour, the average colour was calculated from the lightest and darkest colours.

Modelling

First, an ANOVA (Analysis of Variance) was performed on all different parameters to see whether they significantly differed per site. After testing for homoscedasticity, some parameters were then also tested using a Kruskal-Wallis test, if heteroscedastic. For post-hoc testing, a Tukey's test was used for the ANOVAs, and a pairwise Wilcox test was used for the Kruskal-Wallis tests. Afterwards, parameters were merged in one large dataset, averaging measurements over time, and, if necessary, over plot. For the coral colour, the darkest colour variable was taken. Then, a multivariate ANOVA model was designed to see which parameters explained the response variables (coral colour and growth) the best. First, all variables were tested separately against the response variables. Two separate ANOVA models were also designed for both response variables. All modelling was performed in R Studio.

4. Results

4.1 Abiotic factors

Table 2 Nutrient measurements

Measurement	Stressed	Sand	Degraded reef	Healthy reef
Salinity	29%	30%	29%	29.5%
KH	119.9 mg/l	130.8 mg/l	130.8 mg/l	119.9 mg/l
pH	7	7.75	7.75	7.75
NH4	0 ppm	< 0.05 ppm	< 0.05 ppm	< 0.05 ppm
NO2	0.05 ppm	0.05 ppm	0.05 ppm	0.05 ppm
Phosphate	5 ppm	5 ppm	5 ppm	5 ppm
Total hardness	425 ppm	425 ppm	425 ppm	425 ppm
NO3	1 ppm	1 ppm	1 ppm	1 ppm

As the abiotic factors were only measured twice, a statistical analysis was not performed. The average values are displayed in table 2. No differences between sites were found in terms of sedimentation (ANOVA, $p > 0.1$). See Fig. 22 in the appendix.

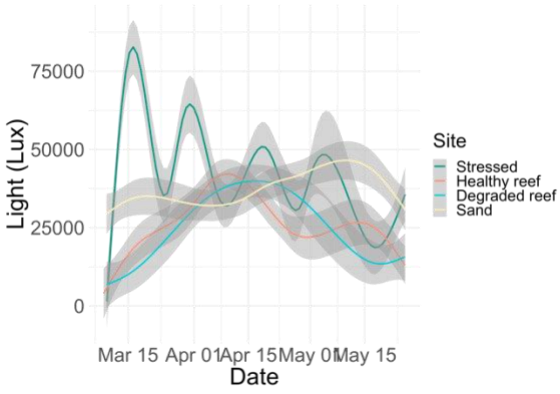

Figure 12 Light over time per site (n(site) = 4)

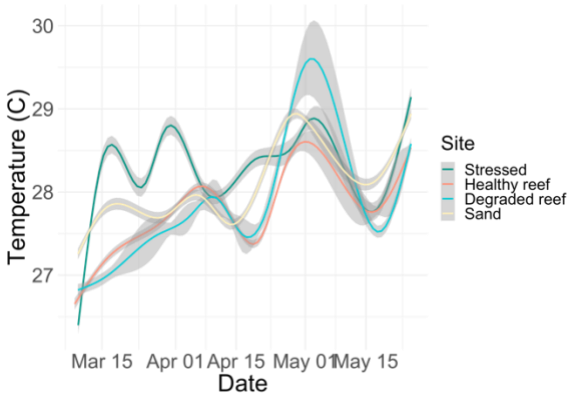

Figure 13 Temperature over time per site (n(site) = 4

Differences were found between the stressed site and the degraded reef and healthy reef sites in terms of light (ANOVA, $p << 0.05$). Differences were also found between the sand site and the healthy reef and degraded reef sites (ANOVA, $p < 0.05$). No differences were found between the sand and stressed site (ANOVA, $p = 0.574$), and between the degraded reef and healthy reef sites (ANOVA, $p = 0.985$). See Fig. 12. Differences were found between the stressed site and the degraded reef and healthy reef sites in terms of temperature (ANOVA, $p << 0.05$). Differences were also found between the sand site and the healthy reef and degraded reef sites (ANOVA, $p << 0.05$). No differences were found between the sand and stressed site (ANOVA, $p = 0.554$), and between the degraded reef and healthy reef sites (ANOVA, $p = 0.864$). See Fig. 13.

4.2 Biotic factors

The average seagrass cover was 2,4% and the average canopy height was 3,5 cm. The healthy reef site had a higher algae cover than all other sites (Kruskal-Wallis, $p < 0.05$). No differences between the stressed, degraded and sand sites (see also Fig. 21 in the appendix).

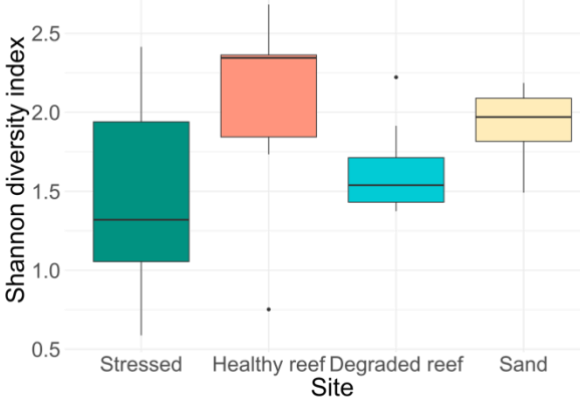

Figure 14 Shannon diversity index per site (n(site) = 4)

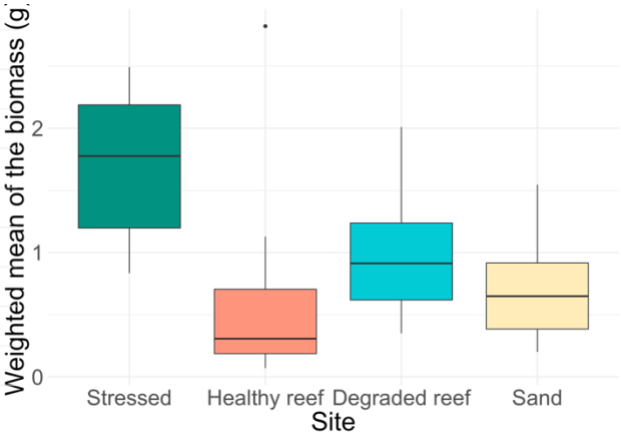

Figure 15 Weighted mean of the biomass per site (n(site) = 4)

The stressed site differs from the healthy reef site and the sand site in terms of Shannon diversity (ANOVA, $p = 0.016$ and 0.048, respectively). No differences between the other sites (ANOVA, $p > 0.1$). The Shannon diversity index was lowest on the stressed site(s) (Fig. 14).

No differences between sites and guilds were found when looking at the biomass (ANOVA, $p > 0.1$). See Fig. 23 in the appendix. In terms of the weighted mean of the biomass, the stressed site differed from all other sites (ANOVA, $p<0.05$). The weighted mean of the biomass was highest in the stressed site(s) (Fig. 15).

4.3 Coral growth and colour

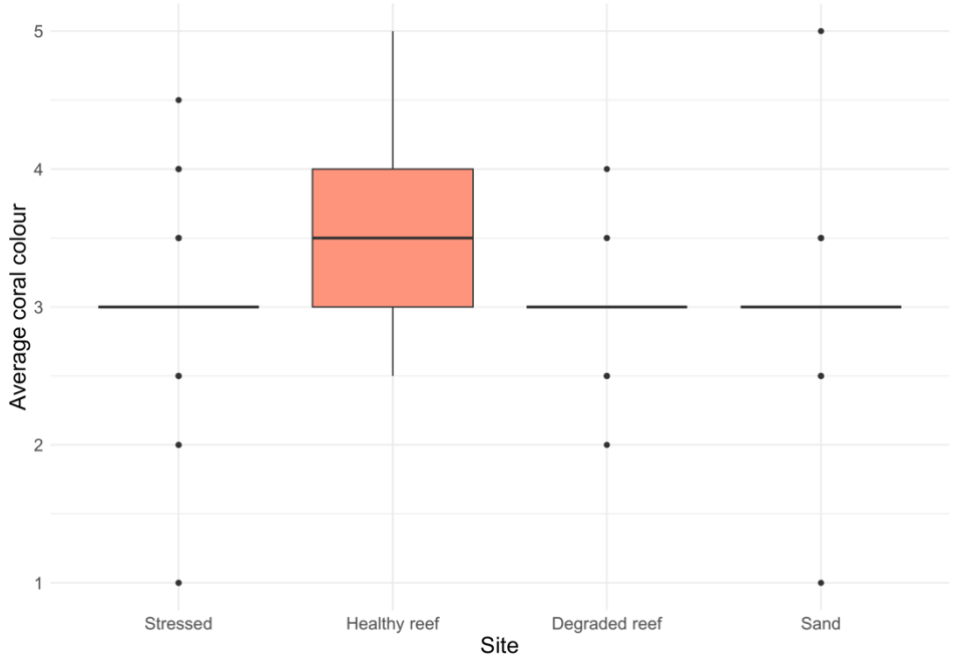

Figure 16 Average coral colour per site (n(fragment) = 120)

All sites differ from each other (Kruskal-Wallis, $p < 0.05$). Average coral colour was highest on the healthy reef site and lowest on the stressed site(s) (Fig. 16).

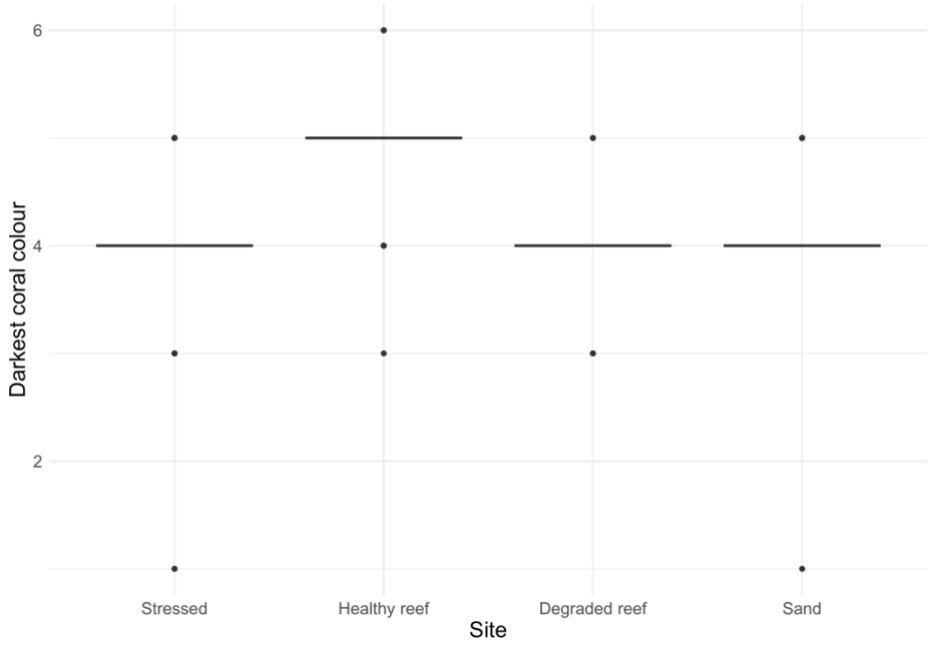

Figure 17 Darkest coral colour per site (n(fragment) = 120)

All sites differ from each other (Kruskal-Wallis, $p < 0.05$) except stressed and sand (Kruskal-Wallis, $p = 0.84$). The darkest colour was highest on the healthy reef site (Fig. 17).

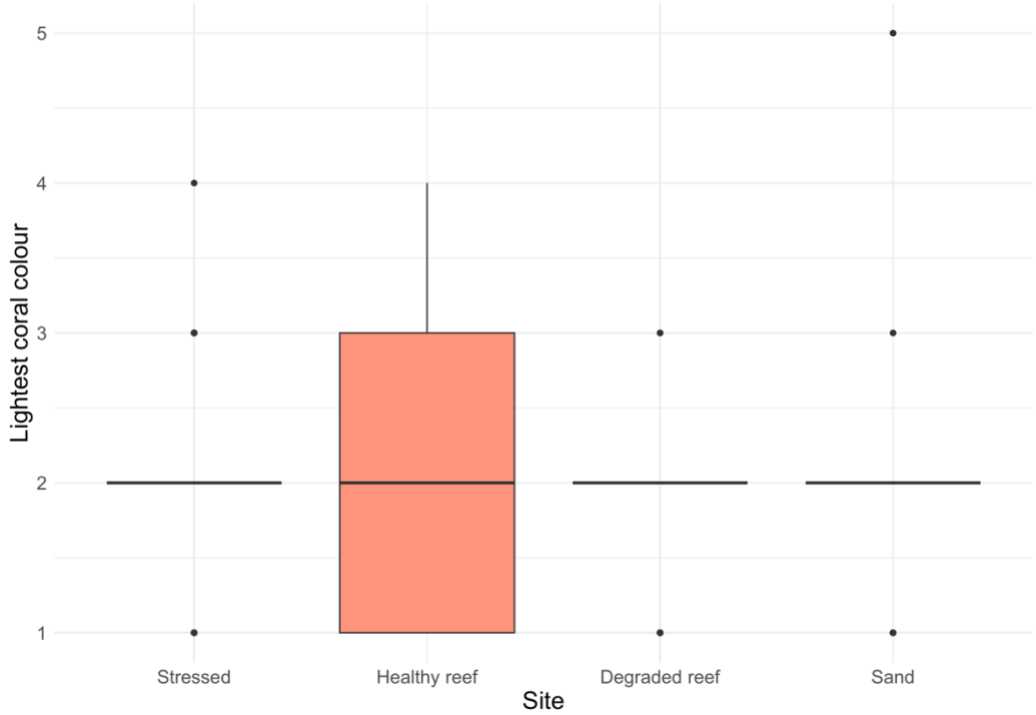

Figure 18 Lightest coral colour per site (n(fragment) = 120)

None of the sites differ from each other (Kruskal-Wallis, $p > 0.1$) except between stressed and sand (Kruskal-Wallis, $p = 0.016$). See Fig. 18.

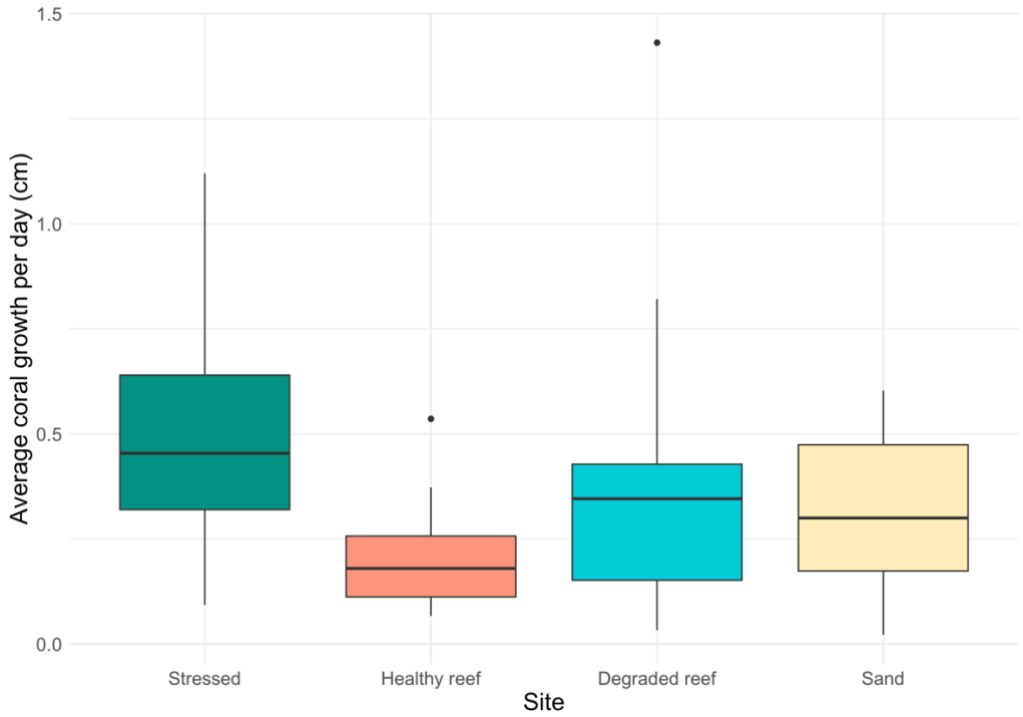

Figure 19 Average cumulative coral growth/day per site (n(fragment) = 120)

No differences between sites were found (ANOVA, $p > 0.05$). See Fig. 19.

4.4 Statistical models

Separate MANOVAs were made for each variable to test them against the response variables.

Table 3 p-values for MANOVAs per parameter

Parameter	**p for growth**	**p for colour**
Sedimentation	0.004146	9.652e-11
Algae cover	0.07569	0.0002429
Light	0.2275	0.1768
Temperature	0.2934	0.3105
Biodiversity index	0.01504	1.214e-05
Total biomass	0.208	6.412e-05
Weighted mean of biomass	0.08263	0.06426
Herbivore proportion biomass	0.1035	0.0003172

Looking at the above multivariate ANOVA models (table 3), the five parameters explaining the coral colour were: sedimentation, algae cover, biodiversity index, total biomass and the herbivore proportion of the biomass. For coral growth, only sedimentation and total biomass seem to be able to explain the variation.

Some MANOVA models were also designed with different combinations of explanatory variables, but the results were inconclusive. The only explanatory variable that had a consistent outcome was the sedimentation rate, this was always significant for both response variables.

When making a model using the two parameters that were significant for both response variables, the sedimentation and the biodiversity index, the following results were found (table 4).

Table 4 p-values for combined biodiversity and sedimentation MANOVA

Parameter	**p for growth**	**p for colour**
Sedimentation	0.004344	1.796e-14
Biodiversity index	0.462145	1.647e-07

When making separate ANOVAs, similar results were found.

5. Discussion

5.1 Abiotic factors

The sites did not differ in nutrient concentrations. They did differ in light and temperature, showing a clear grouping of the sand and stressed site, and the healthy and degraded reef sites. The sand and stressed sites had more light and a higher temperature than the healthy and degraded reef sites. The sites did not differ in terms of sedimentation.

As no statistical analysis could be performed on the nutrient measurements, no definite conclusions can be made. However, for most nutrients, the measured values were the exact same for all sites, so for this specific research it has been assumed that the nutrients did not have an impact on the differences between the sites.

For the light and temperature, a split can be seen, grouping the four sites into two groups of two. The sand and stressed sites did not differ from each other, and neither did the degraded and healthy reef sites, but the two groups (sand and stressed, and degraded and healthy) did differ from each other. This is possibly because the sand and stressed sites, as mentioned before, were quite close to each other after the move of the stressed corals. Additionally, the sand and stressed sites were both shallower (between 4 and 5 m depth) than the other two sites, and this is true before and after the move of the stressed corals. The healthy and degraded reef sites were both situated slightly deeper, between 6 and 7 meters. This could explain the differences in light and temperature. The differences in light and temperature between sites are in line with the hypothesis and earlier research done by Hughes et al. (2017).

The sedimentation rate did not differ between sites. This is not in line with the hypothesis and the results found by Golbuu et al. (2011a). Though this might just simply be because most of the sites were situated in the same bay and the differences might be too small to measure, Fig. 22 does seem to show some differences between the sites. Because the sedimentation traps used had very small openings, the amount of sediment in each trap was quite small. Additionally, most traps contained many hermit crabs. Though the alive hermit crabs were removed before drying, some sediment might have been accidentally removed as well, and some empty shells did remain in the samples. This might have made some measurements less accurate.

5.2 Biotic factors

The algae cover differed between sites, where the healthy reef site had a higher algae cover than all other sites. The Shannon diversity index was lower on the stressed site compared to the healthy reef and sand sites. No other differences were found in terms of the Shannon diversity. The fish biomass did not differ between sites or between guilds, and neither did the herbivore proportion of biomass differ between sites. The weighted mean of the biomass was higher on the stressed site compared to all other sites. Macrobenthos were only measured once, but a summary is shown in table 5 in the appendix. Seagrass seemed to have a negative impact on the biodiversity but a positive impact on the biomass.

The Shannon diversity index differed between the stressed site and the healthy reef and sand sites, but not between the other sites. This is not in line with the hypothesis. The expectation was that more structural complexity, which is present on the healthy reef, would cause a larger diversity in the fish community, as mentioned in Graham and Nash (2013) and Darling et al. (2017). As the sand, degraded reef and healthy reef sites do not

differ from each other, structural complexity seems to not be an indicator of biodiversity on these sites. Additionally, it was expected that the presence of seagrass, such as the stressed corals experienced at the start of the experiment, would also cause a higher biodiversity. This was not the case, as the biodiversity overall was very low for the stressed site(s). This could be explained by the very low density of seagrass.

The fish biomass did not differ between sites or between guilds. Though this is not in line with the hypothesis, it could be explained. For example, on the healthy reef site, the diversity of fish was quite high, but as coral reefs are nurseries (Knowlton et al. 2021), the fish were probably all relatively small. So even though the abundance of fish might be high in this site, the biomass would still be low because of the individual size of the fish sampled. On other sites, such as the degraded site, the biodiversity and abundance might be lower, but the fish were of larger size. This might explain the fact that there were no differences in biomass between sites.

The weighted mean of the biomass was higher on the stressed site than on all other sites. This could mean that there was a larger number of adult fish found in this location. This is not in line with the hypothesis, however, because seagrass beds are also nurseries for fish (Bertelli and Unsworth 2014).

To further investigate the species composition, the proportion of herbivores was calculated using the biomass, but no differences were found between sites, which was not in line with the hypothesis. Bellwood et al. (2019) and Wilson et al. (2009) showed that differences in coral ecosystems cause differences in the fish community. Possibly the used research methods do not allow for the differences to be visible in the data, or the differences are not significant because most of the sites were situated in the same bay and possibly shared fish populations.

Algae cover was only different on the healthy reef site. This is different from expected, as a high abundance of corals usually means a low abundance of algae (Bellwood et al. 2019). However, the healthy reef site did also show the highest number of bleached corals (table 6), so the algae cover did seem to have an impact on the corals. As the herbivore proportion did not differ between sites, this does not explain this difference in algae cover. Perhaps this effect is explained by a parameter not measured in this study, such as wave action or the depth profile.

As the macrobenthos were only measured once, no statistical analysis could be performed. As can be seen from table 5, there were some differences between the sites, so it could be interesting to further look into the macrobenthos community in future research.

The seagrass cover was very minimal, so the effect might not be measurable. However, the stressed corals, which were on the seagrass site first, did worse than the other corals for several parameters (coral colour, Shannon diversity). This is not in line with the hypothesis and the results found in Purvaja et al. (2018) and Gillis et al. (2014). It cannot be said whether this difference was because the corals were moved, because of some other characteristic of the site, or because of the seagrass. The seagrass study site was not in the same bay as the other study sites, but that is why the nutrients were measured. No clear differences were found in the nutrient measurements.

5.3 Coral growth and colour

Coral growth did not differ between sites, but coral colour did, specifically the average coral colour and the darkest coral colour.

Coral growth did not differ between sites. Though this is not in line with the hypothesis, there could be several explanations for this. Firstly, that the site circumstances simply do not influence the coral fragments in terms of growth, or that the differences are too small to measure. Secondly, perhaps the research method in use did not allow for an accurate sampling method. For example, a 3D object (the coral fragment) was measured in 2D format (a photograph). Therefore, some parts of the fragment were difficult to measure accurately. Additionally, a reference object of known size was photographed next to the fragment in order to set the scale. However, this was not always the same object, and sometimes the object was not held next to the coral, but rather in front of it. This causes inaccuracies and irregularities in the scale and therefore the measurements themselves. Some fragments even showed a rapid negative growth, which was highly unlikely considering the circumstances. Though some coral pieces were indeed fragmented, those fragments were still considered as the same piece, and many more pieces showed negative growth than were fragmented. Additionally, the negative growth was much higher than would be possible by predation, as sometimes the negative growth was higher than the original size of the fragment, resulting in a negative length, which is not possible. Therefore, the negative data points were removed from the dataset. Furthermore, the coral fragments were only measured three times, allowing for these irregularities to have a large impact on the data.

The average coral colour was different between all sites, which confirms the earlier stated hypothesis. As for darkest colour, all sites differed except for the sand and stressed site. This might be because these sites were very close to each other after the stressed corals were moved from the seagrass site.

As for the lightest colour, most sites did not differ from each other, except for the stressed and sand sites. This is not in line with the hypothesis. This might be because the lightest colour registered on the coral watch chart is classified as bleached, and most bleached pieces of coral died after a while. However, where the degraded and healthy reef sites had several pieces of bleached coral very soon into the experiment, the sand site did not until quite late into the experiment. The stressed site started off with some bleaching, but some bleached pieces were removed either by accident or during the move of the corals to the other site. Therefore, the lightest colour measurements might not be very reliable. Most measurements for the healthy and degraded reef registered the bleached and dead pieces of coral, causing a majority of the 'lightest colour' measurements to be the lowest possible outcome. Additionally, there was some data loss due to the removal of bleached pieces from the stressed site. As the average colour was calculated from the lightest and darkest colour, for the modelling the darkest colour measurements were used, because the lightest colour measurements were deemed unreliable.

5.4 Statistical models

The results of the modelling were not very conclusive. Sedimentation rate seems to predict both of the variables. This is in line with the hypothesis and the research done by Golbuu et al. (2011a). However, the testing done on the sedimentation dataset showed that there were no differences between sites. Therefore, it could be a good predictor of coral growth, where no differences were found between sites. It could not be a good predictor for coral colour, as there differences were found between sites. Additionally, biodiversity index seems to explain both variables as well, but here the opposite is true: differences were found between sites for the biodiversity index, so it could explain the differences in coral

colour, but not those in coral growth. It is in line with the hypothesis, Graham and Nash (2013) and Darling et al. (2017), stating that the biodiversity would differ between sites.

As for the coral colour, the algae cover, total biomass, and herbivore proportion also explained the variation. As the algae cover was higher on the coral site, and the darkest colour was also highest on the coral site, this is not in line with the hypothesis. As Wilson et al. (2008) and Bellwood et al. (2019) showed, a higher algae cover generally means a decline in coral cover and health. As for the two biomass parameters, neither differed per site, so they cannot accurately explain the variation in coral colour.

5.5 Limitations

Because some of the variables were measured as time series, the different measurements cannot be seen as independent. Therefore, the averages were calculated over time for the MANOVA analysis, though this does mean some measure of data loss. As not all measurements were time series, this was the best possible option for the current research. For some variables, such as the coral colour, each measurement was seen as independent when analysing the differences between sites using ANOVA. This was the best possible option within the scope of this research.

Additionally, some of the data could be considered nested within each other. Firstly, within each site, the coral fragments were grouped on five different structures, meaning that the coral fragments on each structure were not independent from each other. Next to that, the different structures were usually less than a meter apart from each other, meaning that the different structures were also not independent from each other. Though it is possible to account for nested data when doing MANOVA modelling, this was not doable in the scope of this research.

Finally, as mentioned before, the so-called “stressed” corals were moved halfway through the experiment. Not only did this mean that the new stressed site overlapped with the already existing sand site, but it also meant that many environmental factors changed for these coral fragments halfway through the experiment. Though this did offer an opportunity to study the effect of moving the coral fragments, it did make some of the data difficult to interpret, especially while working with time series.

5.6 Future research

Overall, a main point for future research is this: either all parameters should be measured as a time series, or none of the parameters. That way, there is no data loss and an equal number of observations for all parameters. A longer duration of the data collection period would be beneficial for this. If this is done, a statistical model more equipped to handle time series could be used.

As for the selection of sites, more exploration should be done beforehand. For example, not all sites were at the same depth, which influenced the data. Additionally, some sites were quite close to each other, which may have caused interdependency. Also, the plots within the sites were too close to each other to be independent.

As for future endeavours in terms of coral restoration, it could be interesting to look at more different species of corals. Using different species of corals could increase the structural complexity on nursery reefs. It could also be beneficial to not only classify sites by “degraded” or “healthy”, but to assess the structural complexity in more depth. Curacao might not be the best location for this specific type of research, as the coral cover has declined so drastically.

Additionally, the effect of movement stress could be further investigated, as it seems to have some impact, but the impact is not clear from the current research.

Coral measurements

For future research, a specific object should be used, such as a dive slate with a raster on it, or a waterproof ruler. This object should always be placed at the same distance from the coral fragment, and the photograph should always be taken from the same angle, preferably an angle where the largest amount of measurable area is visible. Alternatively, the coral fragments could be measured in situ. Due to the limited use of scuba diving, this was not possible in the current research, but in future research measurements could be easily done while scuba diving, using a flexible measuring tape. If taking measurements of all individual branches of the coral fragment is not feasible in terms of time, the linear size could also be taken. Additionally, the fragments should be measured more frequently and over a longer period of time. Additionally, no bleached pieces should be removed, and perhaps a 7^{th} class should be added for deceased pieces of coral.

Biotic factors

When using photographs to assess certain things, such as algae cover, a structure could be used to ensure the photograph is always taken from the same angle. This method of plot analysis could also be used in future to assess more parameters, such as coral colour or structural complexity. Also, when using seagrass as an environmental parameter, it could be interesting to look at a gradient of seagrass, using different sites with different coverage percentages of seagrass.

Abiotic factors

More measurements with more precise equipment are advised, for example a pH meter instead of a titration test. Additionally, different containers should be used for the sediment traps, for example 50ml centrifuge tubes. Additionally, the sedimentation traps should be left in the water for longer.

6. Conclusion

To conclude, the sites differed in some of the abiotic factors, namely light and temperature. These factors did not, however, seem to explain the variation in coral growth and colour. The sites also differed in some of the biotic factors, namely diversity index, weighted mean of the biomass and algae cover. Though all these results are in line with the hypothesis, some of them are slightly contradictory. For example, the diversity index was lowest on the stressed site, but the weighted mean of the biomass was highest. Additionally, the healthy reef site had the highest algae coverage and bleached coral pieces.
No differences were found in coral growth, biomass, feeding guild proportion, and sedimentation. This was not in line with the hypothesis. The main factors predicting coral growth were sedimentation and biodiversity index, and the main factors predicting coral colour were sedimentation, biodiversity index, algae cover, total biomass, and herbivore proportion. This was partially in line with the hypothesis. The influence of seagrass on the coral growth and health was unclear, as the seagrass cover was very low, and the corals that were on the seagrass site were also submitted to stress.

Overall, one thing seems clear: there are certainly differences between outplant sites, showing that it is important to properly investigate possible outplant locations when starting a new coral restoration project and to consider different environmental factors before deciding on a location.

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Appendix

Table 5 An overview of the macrobenthos community per site

site	macrobenthos community	density	average size (cm)
stressed	shrimp and hermit crabs	5	1,06
sand	worms, shrimp, crab, fireworms	11	1,34
degraded reef	snails, shrimp, fireworm, juvenile fish	7	0,73
healthy reef	shrimp and hermit crabs	4	0,6

As the macrobenthos community was only observed once, a statistical analysis was not performed. A summary is displayed in table 5.

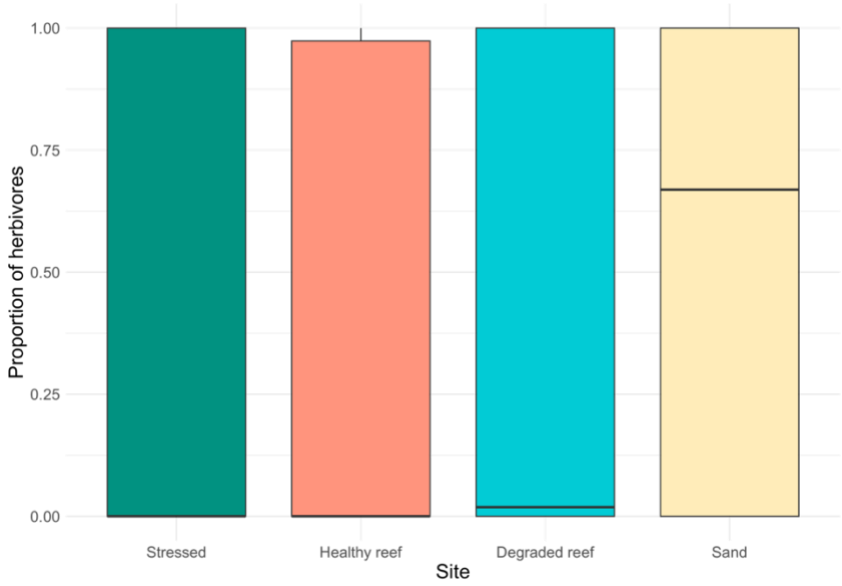

Figure 20 Proportion of herbivores per site (n=4)

No differences were found between the sites (ANOVA, $p < 0.1$). See Fig. 20.

Table 6 Number of bleached pieces of coral per site

site	Number of bleached pieces
Stressed	4
Healthy reef	14
Degraded reef	3
Sand	7

As not all sites had the same number of bleached corals, an overview is displayed in table 6. This is the number of bleached pieces at the end of the experiment.

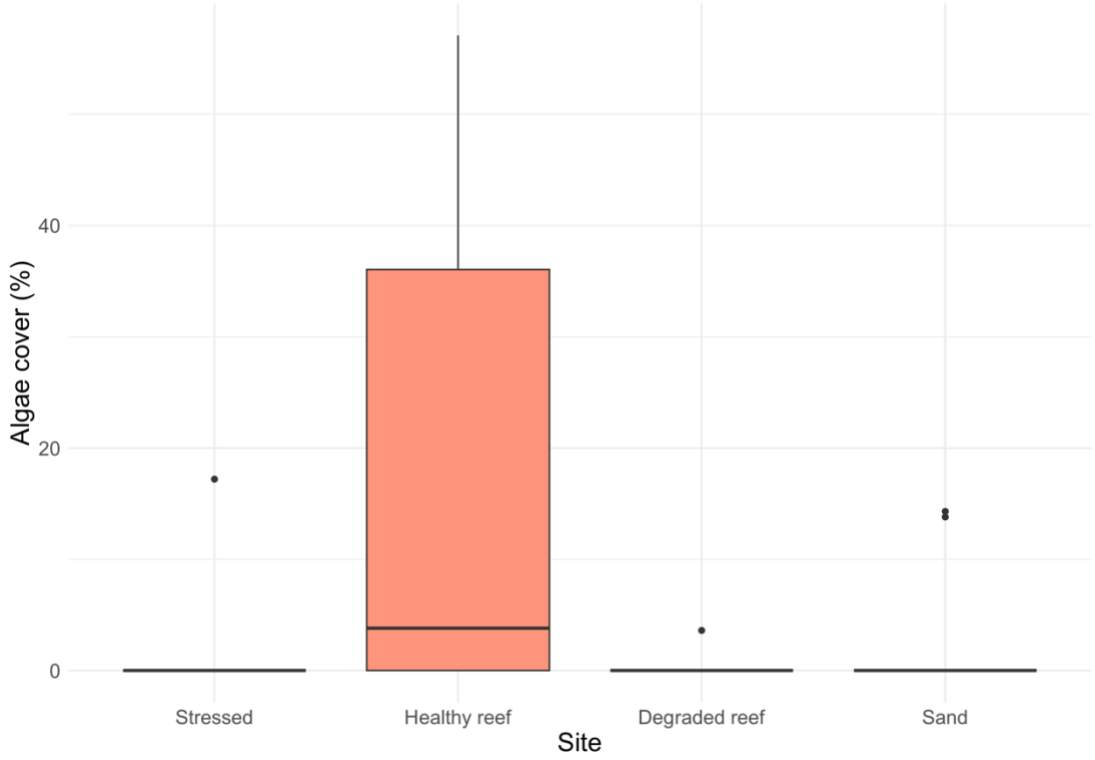

Figure 21 Algae cover per site (n(plot) = 30)

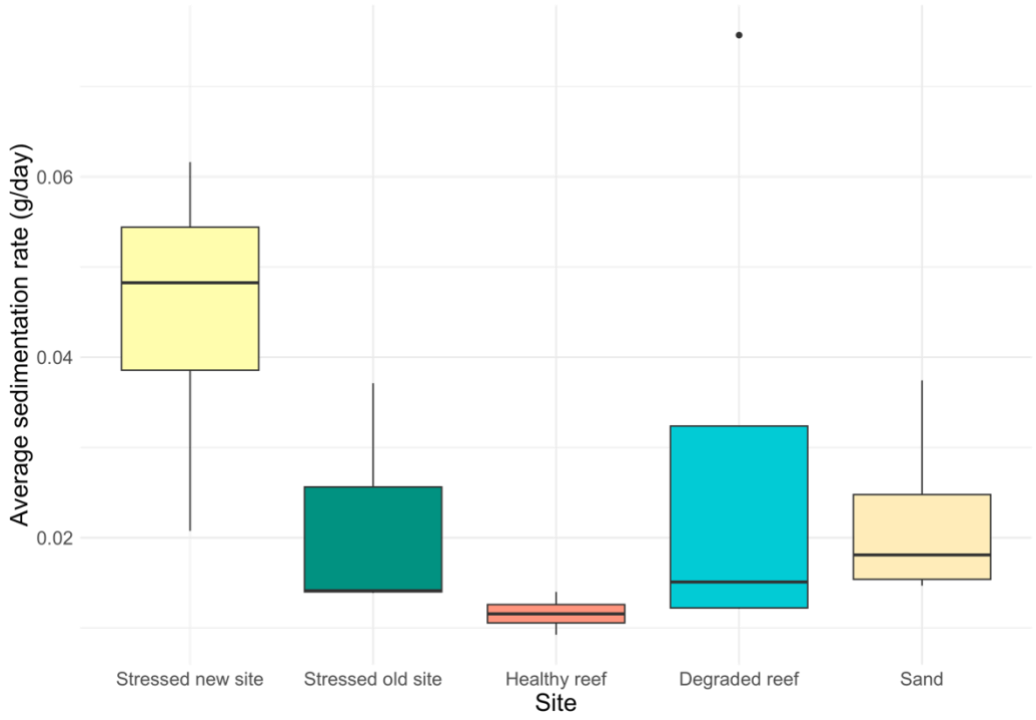

Figure 22 Average sedimentation rate per site (n(sediment trap) = 16)

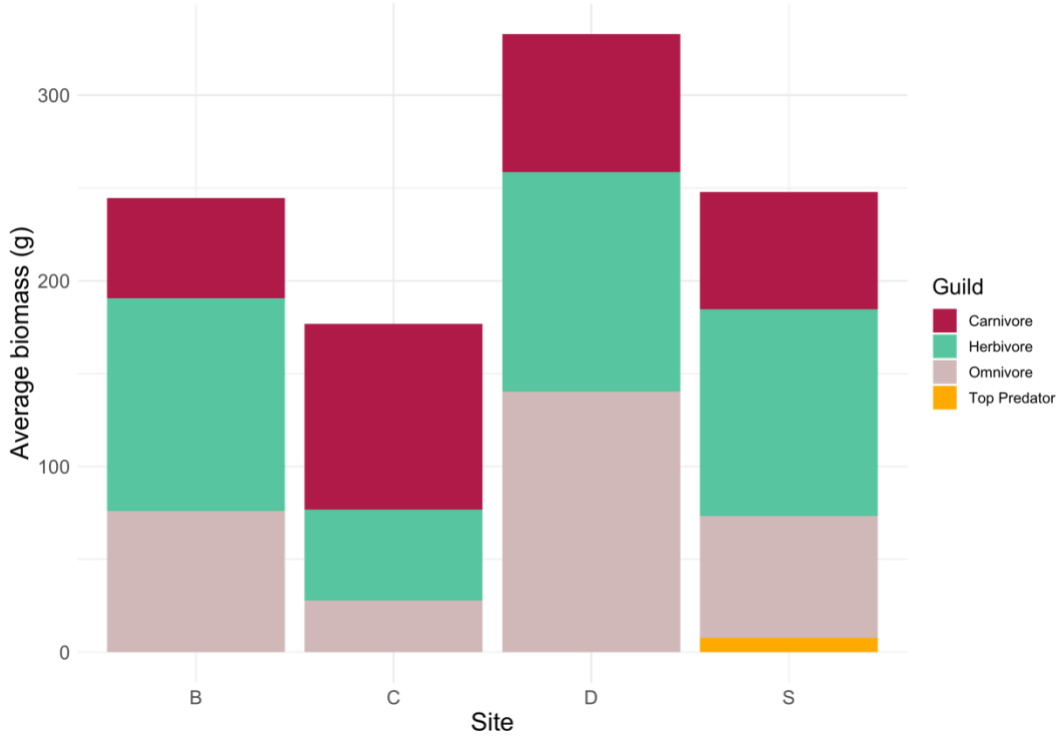

Figure 23 Average biomass per site and feeding guild (n(site) = 4)

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