UC San Diego
Capstone Projects

Title
The Effects of Resource Availability on the Growth and Distribution of a Heterotrophic Coral Species, *Madracis mirabilis*, across Curaçao

Permalink
https://escholarship.org/uc/item/30w6b65r

Author
Cook, Sophie L

Publication Date
2022-07-20

Data Availability
The data associated with this publication are within the manuscript.

The effects of resource availability on the growth and distribution of a heterotrophic coral species, *Madracis mirabilis*, across Curaçao

Sophie L. Cook
Master of Advanced Studies in Marine Biodiversity and Conservation
Scripps Institution of Oceanography, UC San Diego

UC San Diego | SCRIPPS INSTITUTION OF OCEANOGRAPHY

Capstone Advisory Committee:

Dr. Stuart A. Sandin, CAC chair
Professor, Scripps Institution of Oceanography
Director, Center for Marine Biodiversity and Conservation
Principal Investigator, 100 Island Challenge

_____   14 June 2022
Signature / Date

Dr. Brian Zgliczynski
Postdoctoral Researcher, Scripps Institution of Oceanography
Coordinator, 100 Island Challenge

Brian Zgliczynski
Brian Zgliczynski (Jun 15, 2022 08:54 GMT+3)   14 June 2022
Signature / Date

Dr. Mark Vermeij
Science Director, The Caribbean Research and Management of Biodiversity Foundation
Professor of Tropical Marine Ecology, University of Amsterdam

_____   14 june 2022
Signature / Date

Dr. Kate Furby
Tiny Beaker Films, coral reef ecologist

Kathryn Furby (Jun 17, 2022 10:38 PDT)   17 June 2022
Signature / Date

Table of Contents

Abstract

Coral reefs are one of the most biodiverse yet threatened ecosystems on the planet. Our understanding of what contributes to a coral reef's resilience to adapt to global and local threats is not well established. Thriving reefs in close proximity to anthropogenic impacts indicate there are opportunities for improved understanding of the underlying factors that influence the ability of some coral species to withstand environmental stressors and changing oceanographic conditions. Research suggests that resource availability and a coral's trophic strategy can improve a coral's tolerance to environmental stressors. Such discoveries have already been made, but the effects of resource availability on heterotrophic coral species have been minimally explored in the Caribbean; a region that has suffered substantial declines in coral health and cover–. Regardless of these declines, Curaçao, an island in the Southern Caribbean, possesses uncharacteristic coral diversity and cover for the region. One of the most abundant species covering the Curaçao reef tract, *Madracis mirabilis*, is largely heterotrophic in its feeding strategy. The growth and distribution of this species was tracked across 7 sites spanning approximately 40 kilometers along natural and anthropogenic gradients of nutrients in Curaçao. Our findings suggest that the highest growth and percent cover of *M, mirabilis*, can be found in regions with the highest exposure to anthropogenic nutrient loading. These data provide insights into how some corals may be better adapted to changing environmental conditions and degradations in water quality.

Background

Coral reefs are often described by their remarkable biodiversity, supporting one-third of all named marine organisms despite covering less than 0.1% of the ocean floor.[1] Beneficial services provided to people and the planet by coral reefs are vast, contributing to one of the highest economic values annually.[2][3] Benefits range from the tangible: carbon sequestration, coastal protection, food, tourism, pharmaceuticals; to the intrinsic: education, cultural identity and indigenous traditions.[1][2][4] One-seventh of the world's population indirectly benefits from the services provided by coral reefs, while those who heavily rely upon coral reefs for ecosystem services are often some of the most vulnerable to climate change.[2][4]

While being one of the most biodiverse and economically valuable ecosystems, coral reefs are also among the most threatened.[1] Global and local stressors threaten the future of coral reefs, often interacting synergistically to affect their ability to adapt to changing environmental conditions.[1] Global threats include rising sea surface temperatures (SST) and ocean acidification (OA) as a result of carbon emissions, resulting in thermal stress events (bleaching) and the breakdown of calcium carbonate, jeopardizing the reef structure that provides habitat for other organisms.[1] Local threats include overfishing and declines in water quality from anthropogenic pollution entering coastal waters.[5] Historically some of the most pronounced cases of coral decline have been in the Caribbean, with the region acting as a "Canary in the Coal Mine" for the effects of anthropogenic impacts on coral reefs worldwide.[6]

The narrative surrounding the future of coral reefs in the Caribbean is often a dire one. However, corals that grow and survive in spite of the many environmental stressors our oceans face today indicate there is room for improved understanding of how some coral species might be more resilient

[i] to human-related impacts. Gaps in this area of understanding include how a coral's trophic strategy, specifically heterotrophic feeding and resource availability, can improve a coral's tolerance to changing environmental conditions.[7 8 9 10 11]

Corals are mixotrophic organisms, meaning they can meet their nutritional demands both autotrophically (i.e. photosynthesis) and heterotrophically (i.e. consumption of external organic matter).[12 13 14] While corals have been able to form one of the most productive and biodiverse ecosystems in tropical, oligotrophic waters through the assimilation of symbiotic algae to feed autotrophically, corals are also successful carnivorous and herbivorous heterotrophs.[15 16] By feeding on particulate organic matter (POM), dissolved organic compounds, bacteria, and zooplankton, corals can obtain essential nutrients including phosphorus and nitrogen, that cannot be provided to the coral through photosynthesis alone.[13 17]

Trophic plasticity is thought to play a larger role in coral physiology than previously understood, as heterotrophic feeding can support energy reserves and nutritional demands when photosynthesis is inhibited (i.e. bleaching as a result of increased sea surface temperatures, increased turbidity and decreased light attenuation from sedimentation and coastal development).[15] [13] As thermal stress events are likely to increase in frequency and severity in the future from the effects of climate change, heterotrophic feeding might support a coral's survivorship and long-term resilience in the face of changing oceanographic conditions.[10] The ability of a coral to increase its rate of heterotrophic feeding has been shown to positively impact coral physiology through increased calcification, lipid reserves, and tissue growth in some species; and has been observed to improve a coral's tolerance to elevated temperatures and turbidity. [10 18 19 20]

What influences a coral's feeding behavior is not fully understood, but it is thought to be affected by environmental gradients and resource availability.[7 8 9 19] Environmental variability is thought to impact a coral's trophic strategy, as depth and turbidity decrease light attenuation, affecting a coral's ability to derive its nutrition autotrophically via photosynthesis, thus increasing its reliance on heterotrophic feeding.[7 19 21] Resource availability can also be a factor in predicting a coral's dominant trophic strategy. Regions with higher oceanographic primary productivity have been found to be a predictor of trophic strategy in some corals, as resource availability allows a coral to increase its feeding rate.[9] Higher oceanic primary productivity (often measured through surface chlorophyll *a* concentrations), can often be attributed to varying oceanographic conditions, including frequent upwelling events, and can indicate a higher quantity of naturally occurring nutrients present in the water column.[22] Gradients of increased nutrient concentrations enhance the ability of a coral to derive its nutrition heterotrophically, as readily available nutrients can increase phytoplankton abundance, attracting zooplankton for corals to feed upon. [22 23 24] Past observations and studies suggest that a coral's ability to increase its feeding rate in response to available resources in the water column could provide a competitive edge in withstanding environmental stressors.[7 8 9 10 13 25 26]

---

[i] Resilience defined as "the ability of reefs to absorb recurrent disturbances and rebuild coral-dominated systems." Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Introduction

Curaçao, a southern Caribbean island located just 60 km (37 miles) north of Venezuela, represents a case of uncharacteristic coral coverage and taxonomic biodiversity in the Caribbean (*See Figure 1*). [5] [27] [28] [29] [30] In 2012, average coral cover in Curaçao was estimated to be double of that in the broader Caribbean, and the island is considered to possess some of the most biodiverse reefs one can visit in the region. [5] [28] One kilometer of healthy reef in Curaçao is worth approximately $1.6 million per year by providing opportunities for tourism, habitat for fisheries, and coastline protection. [28]
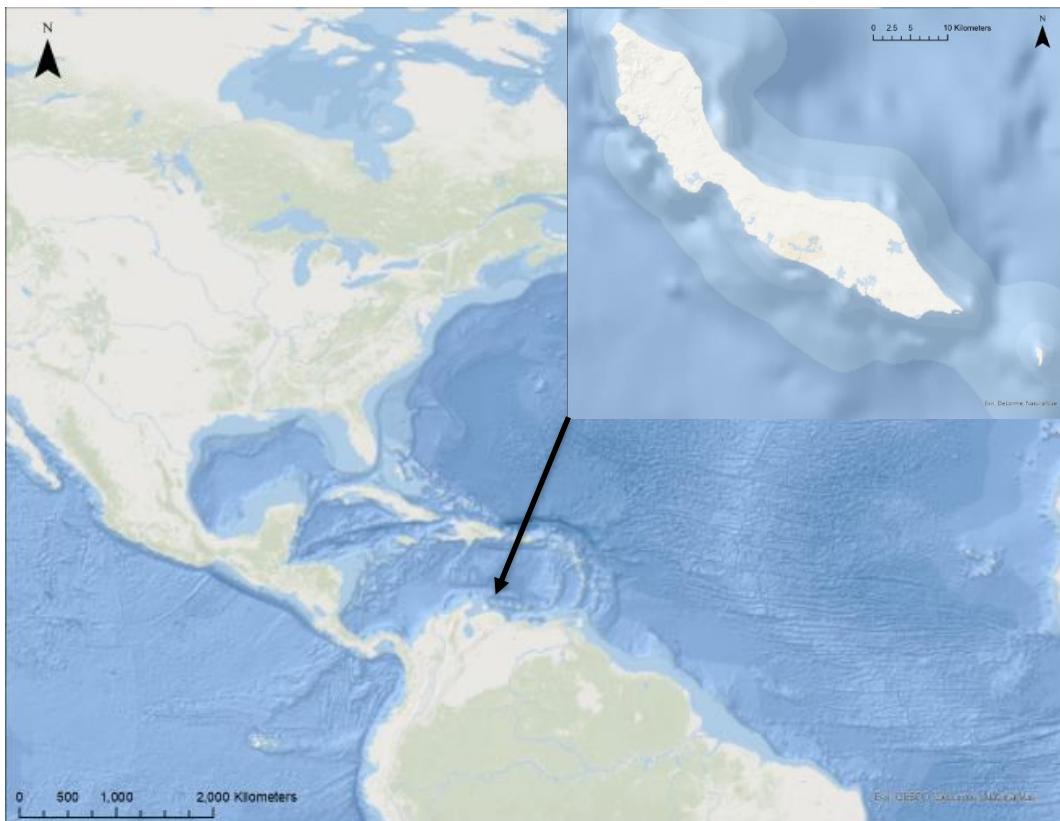
Figure 1 Map of Curaçao

Regardless of their noteworthy health, diversity and value, Curaçaoan coral reefs have not been sheltered from the declines occurring throughout the Caribbean.[29] Between 1982 and 2015, it is estimated that Curaçao lost approximately 50% of its coral cover.[30] Primary drivers of this decline include overfishing and pollution of coastal waters from coastal development. [30] The highest declines in coral cover have been along the leeward coast around the island's capital, Willemstad, where water quality has been affected by sea and land-based pollutants including sewage, run-off, and chemical waste; although it is difficult to distinguish the primary drivers of this decline.[28]

In recent years, *Madracis mirabilis*[ii] (common name: yellow pencil coral) has become one of the most abundant coral species across the shallow forereefs on the leeward coast of Curaçao.[31] *M. mirabilis* is a branching, weedy, opportunistic coral species that is known for its fast, dynamic growth and ability to quickly colonize an open reef tract.[32] The feeding strategy of *M. mirabilis* is considered to be almost exclusively heterotrophic, as it can efficiently feed on zooplankton, bacteria and other particulate matter in the water column. [24][33][34]

It is thought that this opportunistic species of coral is able to grow where other species may struggle to survive. Observations by Bak, et al., (1998) mentioned that despite the decline in other coral taxon across the forereefs of Curaçao, it seemed the "monospecific beds" of *M. mirabilis* remained relatively unchanged in areas downcurrent of coastal development with poor water quality, as its heterotrophic feeding strategy could provide a competitive edge in comparison to other species.[34] Other observations support evidence of this trend, as the abundance of *Madracis spp.* has increased across the reef tracts of Curaçao since 1973, while the majority of other coral taxon have declined (*See Table 1*).

Although anthropogenic nutrient loading and pollution are likely to have contributed to the degradation of many coral reefs, nutrient enrichment can have a wide range of effects on coral physiology and ecosystem health. [35][36][37] Declines in reproduction success, growth, and thermal tolerance are a few of negative physiological impacts that nutrient enrichment and pollution can have on corals.[36][37] Eutrophication of oligotrophic waters, in conjunction with thermal stress and the decline of herbivorous fishes, can contribute to phase shifts as algae outcompete corals for space.[38][39] Other studies have found that the presence of phosphorus and nitrogen, in moderate amounts, can positively impact the growth and thermal tolerance of some corals.[8][40] Moderate concentrations of inorganic nitrogen during thermal stress or elevated levels of CO2 have also been found to support coral growth and metabolism.[41] The effects of nutrient enrichment are likely to be depend on nutrient concentration, the type of nutrient present, and are often species-specific.[42]

Despite the problematic effects of human-caused eutrophication, which are certainly a cause for concern in addressing the many threats to coral reefs, few studies have examined how anthropogenic nutrient loads impact heterotrophic, opportunistic coral species in the Caribbean. We sought to compare how different sources and loads of nutrients predict or are related to the growth and distribution of *M. mirabilis,* a weedy, largely heterotrophic coral, across the shallow forereefs of Curaçao.

Two nutrient gradients were used to look for environmental signaling. Bioassays have become increasingly popular to estimate the relative exposure to anthropogenic pollution a marine habitat has experienced. Stable isotope signatures of $\delta^{15}N$ obtained from samples of macroalgae can provide a relative profile for the amount of anthropogenic nutrient loading that has occurred on or near a coral reef.[43] Nitrogen ($\delta^{15}N$) values were used as a proxy for the availability of anthropogenic nutrients near each of the study sites. Chlorophyll *a* is often used as a measurement of oceanographic primary productivity, with larger concentrations of chlorophyll *a* signaling higher amounts of naturally occurring nutrients (such as nitrogen and phosphorus) and food availability in a given oceanographic region. Chlorophyll *a* was utilized as a proxy for oceanic primary productivity and the availability of naturally occurring nutrients in the water column.

[ii] While *Madracis mirabilis* is commonly referred to as *aurentenra*, other references suggest there is not enough evidence to support the name change from *M. mirabilis* to *M. aurentenra*. For this study, this species of *Madracis* found in the shallow waters of Curaçao will be referred to as *mirabilis.*
See:http://www.coralsoftheworld.org/species_factsheets/species_factsheet_summary/madracis-mirabilis/

Seven reefs were chosen spanning from the northernmost point of the island to a point south of Willemstad, the island's capital, and most heavily populated area. On the windward (eastern) side of the island, reefs are exposed to trade winds and large waves while the leeward (western) side, is more sheltered from strong waves and wind, with protected bays and blue lagoons.[44] [45]

Examining how the growth and distribution of *M. mirabilis* changes in relation to varying nutrient types and loads will offer novel perspectives on how some corals grow and adapt despite the many local and global stressors coral reefs face today.

Table 1 Island wide average of percent cover of coral (10 m depth) across Curaçao

Species	1973[*]	2003[**]	2010[†]	2015[††]
Agaricia spp.	16.5	3.0	3.0	1.8
Colpophyllia sp.	0.6	1.6	1.2	0.7
Dendrogyra cylindrus	0.0	0.2	0.0	0.1
Dichocoenia	0.7	0.0	0.0	0.0
Diploria clivosa	0.4	0.0	0.0	0.0
Diploria labyrinthiformis	0.7	0.7	0.1	0.1
Diploria strigosa	0.0	0.1	0.4	0.7
Eusmilia fastigiata	1.4	0.3	0.3	0.1
Favia fragum	0.1	0.0	0.0	0.0
Madracis spp. (mostly M. mirabilis)	2.6	2.6	4.3	3.1
Manicina areolata	1.1	0.0	0.0	0.0
Meandrina meandrites	0.9	0.3	0.2	0.2
Millepora spp.	0.7	0.8	0.5	1.1
Montastraea annularis s.l.	24.2	12.0	9.1	3.2
Montastraea cavernosa	3.1	0.6	1.2	0.9
Mussa angulosa	0.2	0.0	0.0	0.0
Mycethophyllia spp.	0.3	0.0	0.0	0.0
Porites astreoides	1.7	0.9	1.0	0.5
Porites porites	1.6	0.2	0.2	0.2
Scolymia spp.	0.0	0.0	0.0	0.0
Siderastrea siderea	7.1	0.0	0.5	0.7
Stephanocoenia michelinii	0.4	0.1	0.1	0.1

[*]1973 data: Nagelkerken (1979) PhD thesis island wide averages based on 9 sites/ % cover (original data per site is lost).
[**]2003 data: Vermonden K (2003) Carmabi unpubl. data; island wide averages based on 9 sites.
[†]2010 data: Vermeij MJA (2010) Carmabi unpubl. data; island wide averages based on 21 sites.
[††]2015 data: Waitt Surveys (2015) based on 145 sites.

I. By tracking the change in percent cover of *M. mirabilis* from 2016 to 2020 across different nutrient gradients, what can we learn about the effects of resource availability on the growth and distribution of a heterotrophic coral species in the Caribbean?

II. How do different nutrient gradients affect the growth and distribution of *M. mirabilis*?

    A. How do the patterns of growth and distribution change in areas of high coastal development and anthropogenic nutrient loading with the highest nitrogen ($\delta^{15}N$) values?

    B. How do the patterns of growth and distribution of *M. mirabilis* change in areas of high primary productivity with the highest chlorophyll *a* values?

III. Is there a significant change in growth of *M. mirabilis* at each study site from 2016 to 2020?

Hypothesis

I. *M. mirabilis* will show higher growth rates and percent cover in response to higher resource availability; along gradients of anthropogenic nutrient loading (higher $\delta^{15}N$ values) and natural oceanic productivity (higher values of chlorophyll *a).*

Methodology

Study Sites

Seven 100 m^2 reef plots were chosen along Curaçao's leeward coast, spanning approximately 40 kilometers from North to South, with each site experiencing varying environmental conditions. Monitored sites (from North to South and numbered 1-7 in *Figure 2*) included Westpunt (1), Paradise (2), Playa Hulu (3), Pesh Bay (4), Buoy 2 (5), Water Factory (6) and Seaquarium (7) (*See Figure 2*). These sites were prioritized based upon the availability of temporal and spatial data from the 100 Island Challenge. This study analyzed large-area images collected annually from 2016 to 2020 for each of the sites. For details on the large-area image collection methods please see Edwards et al., 2017 and Kodera et al., 2020.[46] [47]
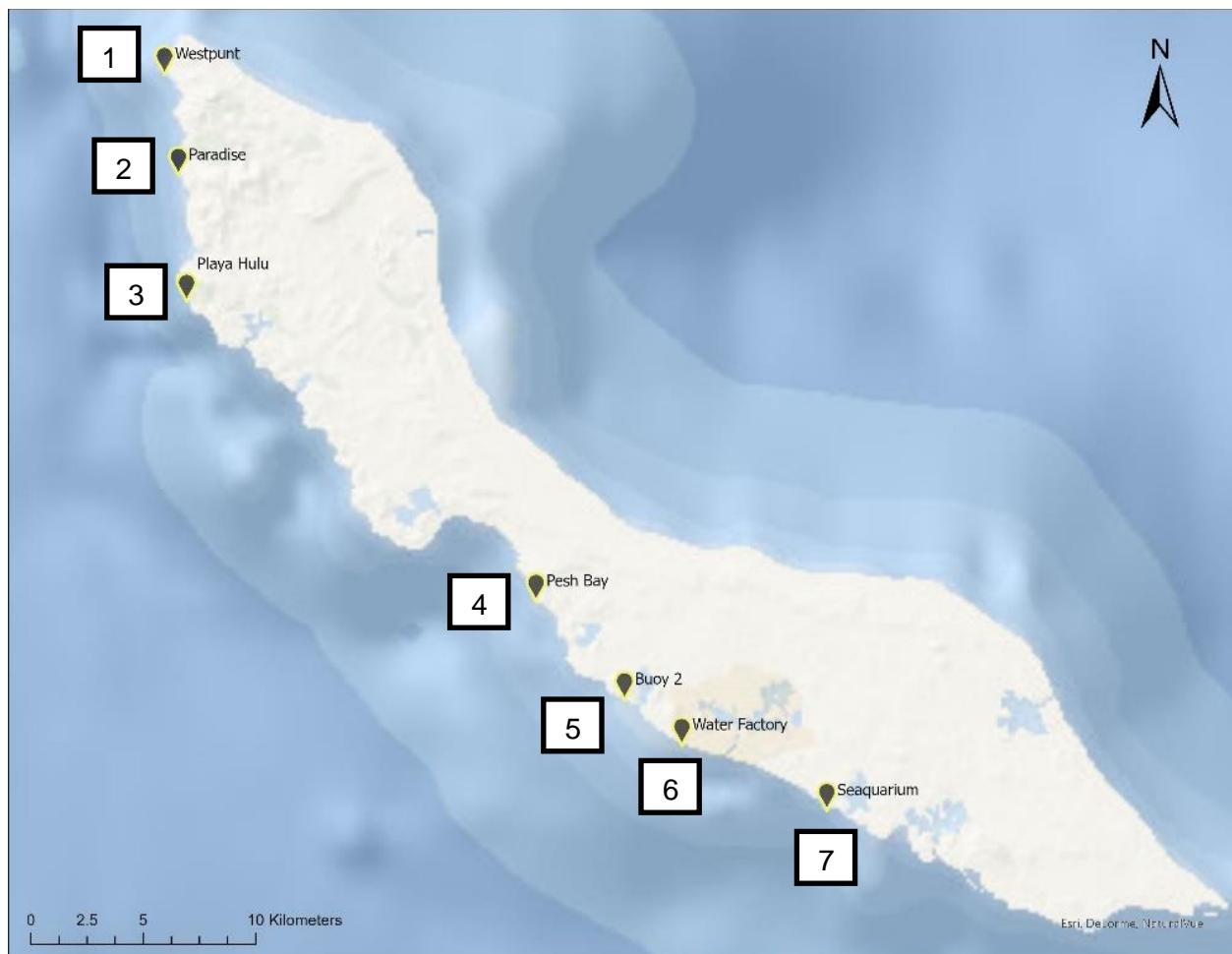
Figure 2 Map of sites studied along the leeward coast of Curaçao

Environmental Variables Used

Environmental data including mean chlorophyll *a* values and a pollution proxy ($\delta^{15}N$) were taken from a 2015 study by Sandin et al., that collected environmental data from 122 sites along a 70 km expanse in Curaçao.[48] These nitrogen and chlorophyll *a* data were used to examine the effects of anthropogenic and naturally occurring nutrients on the growth and distribution of *M. mirabilis* across the 7 study sites.

Prior studies have used chlorophyll *a* concentrations as a predictor of trophic strategy in corals, with higher rates of heterotrophy at locations with higher primary productivity and resource availability.[9] Chlorophyll *a* was used as a proxy for naturally occurring nutrients in the water column and greater food availability for heterotrophic feeding. Chlorophyll *a* values (mg m$^{-3)}$ were acquired from the 2015 CORE study in Curaçao, which calculated an 11-year mean from 2005 to 2015 from the Moderate Resolution Imaging Spectroradiometer (MODIS; https://modis.gsfc.nasa.gov/data/).[48]

A proxy to determine anthropogenic nutrient loading was estimated through the $\delta^{15}N$ stable isotope signature of *Dictyota spp.* samples collected during the 2015 CORE study in Curaçao.[48]

Nitrogen ($\delta^{15}N$) signatures from each alga sample provided a profile for the relative exposure to anthropogenic inputs of nutrients near each of our study sites. To differentiate if the nitrogen values were anthropogenically or naturally derived, we used the parameters described by

Lapointe et al., (2004) and Dailer et al., (2010) to detect the amount of anthropogenic impact each site experienced. Samples of macroalgae collected from coastal waters that had been chronically impacted by anthropogenic sources of nitrogen (e.g. wastewater and sewage) typically had $\delta^{15}N$ signatures greater than 3‰, while $\delta^{15}N$ signatures of macroalgae collected from "relatively unpolluted" oligotrophic waters had a mean of 0.5 – 1.0‰.[49] Further estimation of nitrogen signatures were estimated to be greater than 3 ‰ that were related to sewage and wastewater, between 1 - 3‰ for agricultural nitrogen, and less than 0.5‰ for natural nitrogen fixation.[49] A second study found that average $\delta^{15}N$ signatures for areas impacted by sewage ranged from 4 - 25‰, and signatures between 2 - 3.5‰ were suggestive of agricultural inputs of nitrogen.[43] In a similar fashion, we estimated that $\delta^{15}N$ signatures greater than 1.5 - 2‰ were indicative of anthropogenic impact (including both agricultural runoff and sewage) in our sites.

Taxa Studied

The predominant trophic strategy of *M. mirabilis* is considered to be heterotrophic.[24] For this reason, *M. mirabilis* was chosen to see how resource availability over different nutrient gradients may affect its growth and distribution. The branching colonies of *M. mirabilis* are characteristically fragile, often breaking into many small pieces before undergoing rapid growth by initially forming small, hemispherical colonies.[32] For the purpose of this study, we were interested in shifts in total planar area and percent cover of the study species rather than changes in individual colony growth.

Technologies and Software Utilized

Large-area imagery collected during the 100 Island Challenge presented a unique opportunity to study digitized snapshots of Curaçao's reefs through time. Structure from Motion (SfM) photogrammetry has become increasingly popular over in-situ benthic surveys, as data collected serve as a digital archive for subsequent ecological and biological surveys to be conducted long after the initial collection of data.[50] Using photogrammetric methods to study marine habitats reduces the effort needed to extract high-resolution temporal and spatial data, and reduces user error as data including taxonomic identifications can be cross-referenced as opposed to in-situ surveys conducted on SCUBA.[51][52]

Viscore

Viscore, a point-based visual analytics engine, is a software that allows users to work with three-dimensional models of benthic habitats such as coral reefs.[53] The ability to visualize coral reefs as three-dimensional models allows the user to ask and answer ecological questions about how these ecosystems are changing through time. Structural metrics such as rugosity can be calculated from the three-dimensional models, or the models can be orthoprojected into two-dimensional planar images to analyze growth, percent cover, abundance, among other measurements. Models from different timepoints can be co-registered to observe ecological changes through time.[54]

Once final sites and models were selected, models for each timepoint were checked for proper orientation and scale before being aligned and co-registered with models from other timepoints. Each three-dimensional model was orthoprojected in Viscore to create a high resolution, two-dimensional, planar image of each reconstructed reef to be uploaded into TagLab.[54]

The two-dimensional planar images (also referred to as orthoprojections) created from the three-dimensional models in Viscore were uploaded into TagLab for data processing. TagLab is a software program designed for the annotation and segmentation of benthos where data regarding growth and percent cover can be extracted from the imagery.[55]

The orthoprojections were organized by site and year in TagLab to create a timeseries for individual sites. Uploaded timeseries were used to track the annual growth of *M. mirabilis* from 2016 to 2020. Plots of 100 m^2 were placed in the center of each map, covering the same area of reef through time for spatial continuity. Only *M. mirabilis* colonies within this plot were annotated and segmented while areas that extended beyond this plot were omitted (*See Figure 3*).
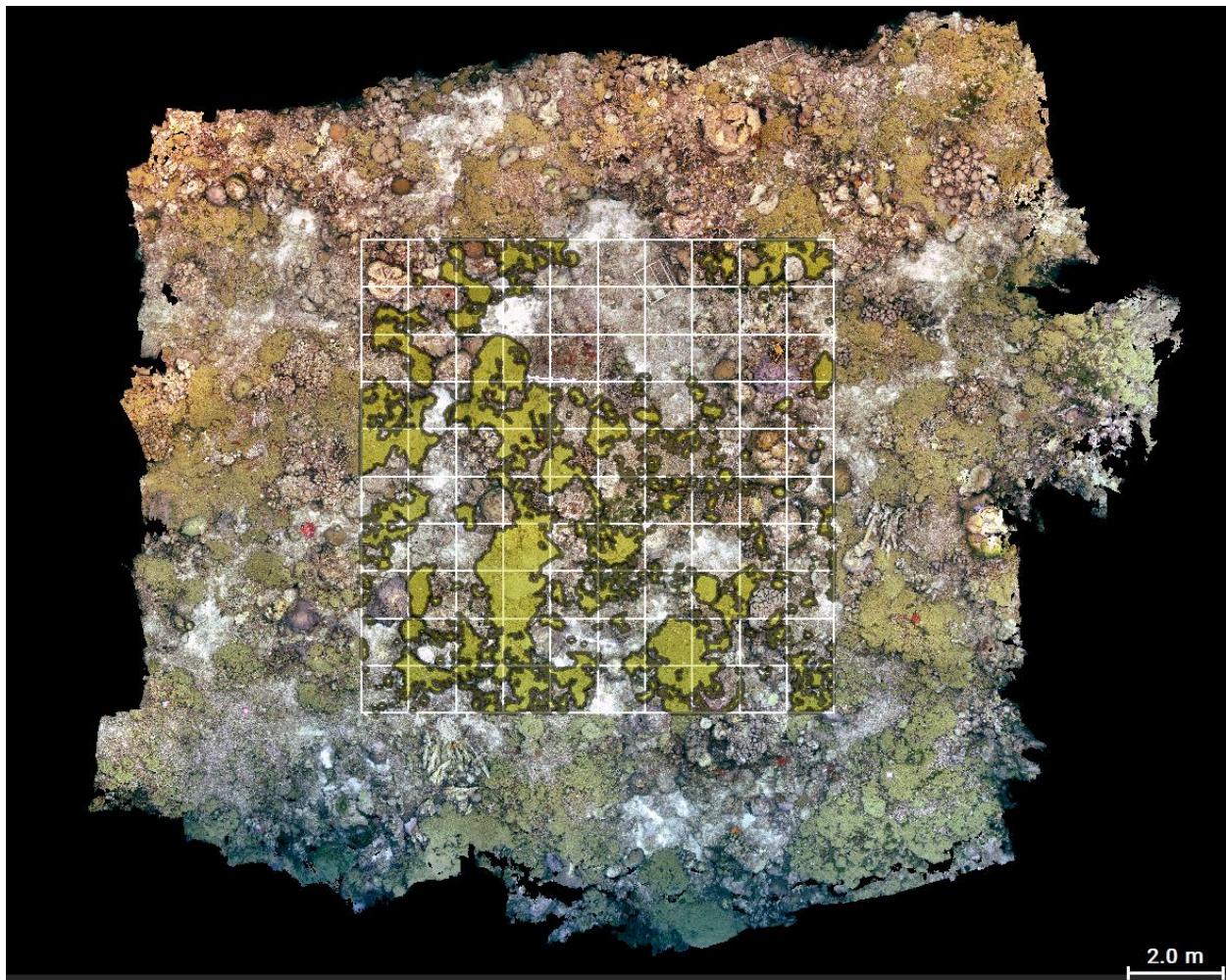
Figure 3 Snapshot of a 10 m x 10 m plot (Seaquarium, 2016) used to track M. mirabilis *through time. The yellow patches are the annotated and segmented colonies of* M. mirabilis.

Due to the difficulty in determining what constitutes an individual colony of *M. mirabilis*, total planar area (m^2) (converted into percent cover) of the study species within the 100 m^2 plot was used as a metric for growth rather than tracking colony growth through time. Patches smaller than

10 cm in length were not traced. Areas with exposed skeleton, algae, or holes in the imagery larger than 10 cm in length were cut out of each segmentation.

Quality Control

Annotations in TagLab were compared to raw imagery of reconstructed models in Viscore to ensure proper taxonomic identification and segmentation of *M. mirabilis* patches. Comparison to raw images assured that annotations were properly labeled and/or identified, and that segmentations only included healthy, live tissue of *M. mirabilis*.

Data Processing

Post quality control, data were extracted from TagLab as .csv files to be processed and analyzed in Microsoft Excel. The output of extracted data from TagLab provided the planar area (m^2) for each annotated patch of *M. mirabilis.* Total planar area (m^2) covered by *M. mirabilis* was calculated by summing together the planar area (m^2) for all individual patches within each timepoint.

Using these data, the percent cover of *M. mirabilis* for each timepoint within each $100m^2$ plot was calculated. Annual percent cover of *M. mirabilis* was calculated by dividing the total planar area (m^2) for the year by the plot area ($100m^2$) to get percent cover. From these data, the average percent cover of *M. mirabilis* from 2016-2020 for each site was calculated for further analysis.

Esri ArcGIS

Using ESRI ArcGIS maps, feature layers were created to visualize values of primary productivity (chlorophyll *a*) and anthropogenic nutrient loading (δ^{15}N as the pollution proxy) to compare environmental conditions and the percent cover of *M. mirabilis* across Curaçao. These maps allowed us to look for potential environmental signals influencing the growth and distribution of *M. mirabilis.*

A 1 km buffer was added around each site studied to obtain the values for δ^{15}N and chlorophyll *a* proximal to each site. Only values within each buffer were taken to calculate the average nutrient load for each site.

Statistical Analyses

Linear regressions were performed to test the null hypotheses of each research question addressed by this study. The first regression sought to identify a potential relationship between anthropogenic nutrient loads and the average cover of *M. mirabilis*, by testing the null hypothesis that nitrogen (δ^{15}N) has no effect on the average percent cover (see research question 2A). A second regression was used to identify a potential relationship between chlorophyll *a* concentrations and the average cover of *M. mirabilis,* with the null hypothesis being that oceanic productivity (chlorophyll *a*) has no effect on the average percent cover (see research question 2B). A third series of linear regressions were performed for individual sites, to see if there was a significant change in growth of *M. mirabilis* from 2016 to 2020, with the null hypothesis being that the growth of *M. mirabilis* is not significant through time (see research question 3). Significance was calculated using Excel's Linear Regression Data Analysis Toolpak.

Results

Relationship between Environmental Variables and Percent Cover of Madracis mirabilis

We hypothesized that the average percent cover and growth of *M. mirabilis* would be the highest in sites along resource gradients with the highest availability of nutrients. It was expected that the highest percent cover and growth would be found in both naturally productive waters where chlorophyll *a* concentrations were the highest and in areas altered by sources of anthropogenic nutrients with high δ^{15}N values.

Overall, the percent cover of *M. mirabilis* generally increased moving from North to South along the leeward coast. The highest percent cover was found among the sites Buoy 2, Water Factory, and Seaquarium; and the lowest percent cover was found among the sites Westpunt, Paradise, Playa Hulu, and Pesh Bay (*Figure 4*).

Our findings revealed that the average percent cover of *M. mirabilis* was the highest in the southern sites where nitrogen (δ^{15}N) values were the highest. (*Figure 5*). Inversely, average percent cover of *M. mirabilis* was the lowest among the northern sites where chlorophyll *a* concentrations were the highest (*Figure 6*).

Linear regressions revealed a positive relationship between anthropogenic nutrients (δ^{15}N) and the percent cover of *M. mirabilis* ($R^2 = 0.5269$, p = 0.064) (*Figure 7*). A second regression showed a weak negative relationship between chlorophyll *a* concentrations and average percent cover of *M. mirabilis* ($R^2 = 0.3718$, p = 0.145) (*Figure 8*).
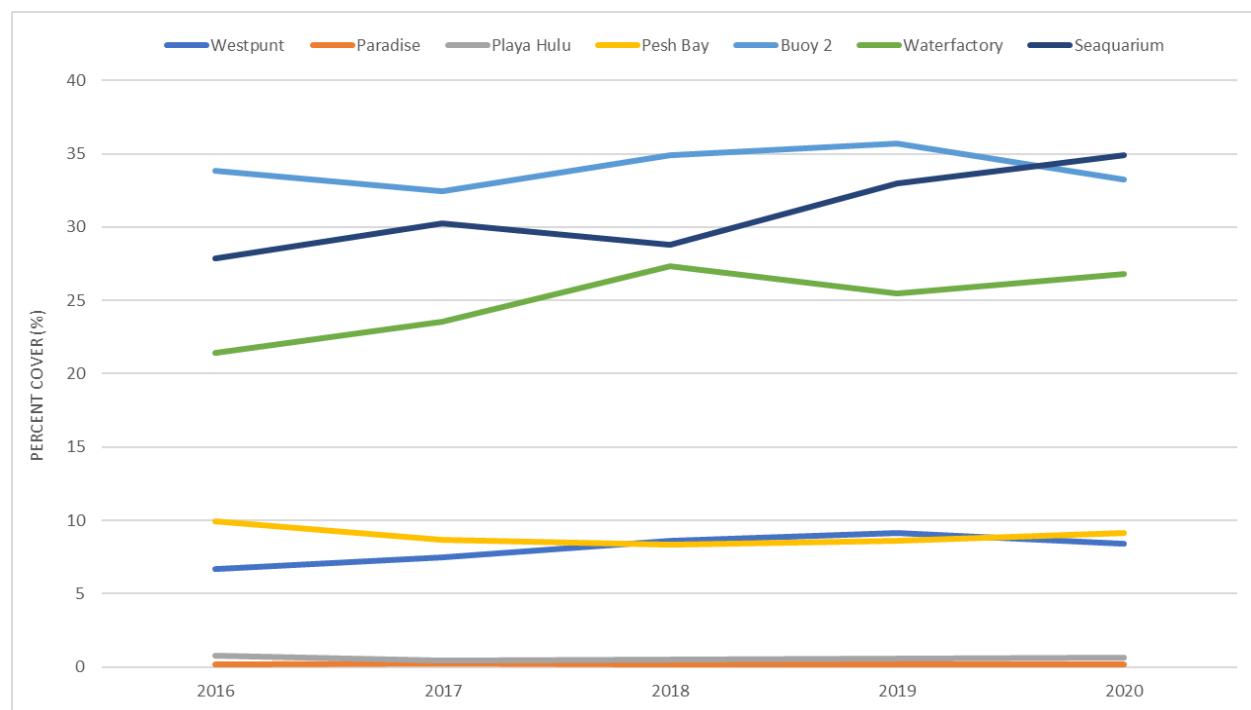

Figure 4 Percent cover of M. mirabilis *by year and site. The highest percent cover was found in the southernmost sites (Pesh Bay, Buoy 2, Water Factory And Seaquarium). The lowest percent cover was found in the northernmost sites (Westpunt, Paradise, and Playa Hulu).*
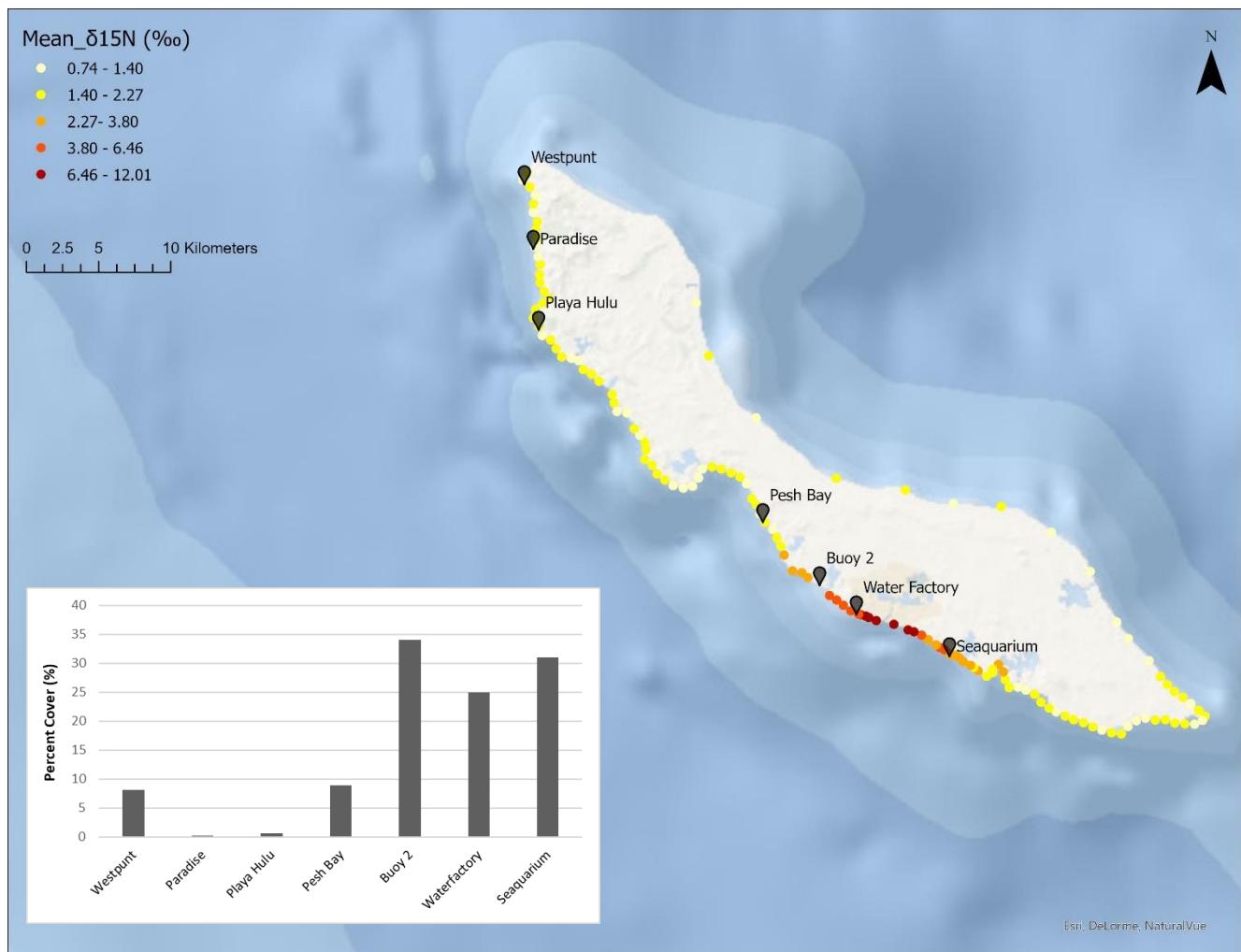
Figure 5 Distribution of sites studied and approximate pollution proxy values (δ15N). Average percent cover of M. mirabilis *was highest in the southeastern sites (average percent cover ranged from 24-34% for Buoy 2, Water Factory and Seaquarium) where δ15N concentrations are the highest (average $\delta^{15}N$ values ranged from 3.4 – 6.7 ‰ in the southeastern sites).*
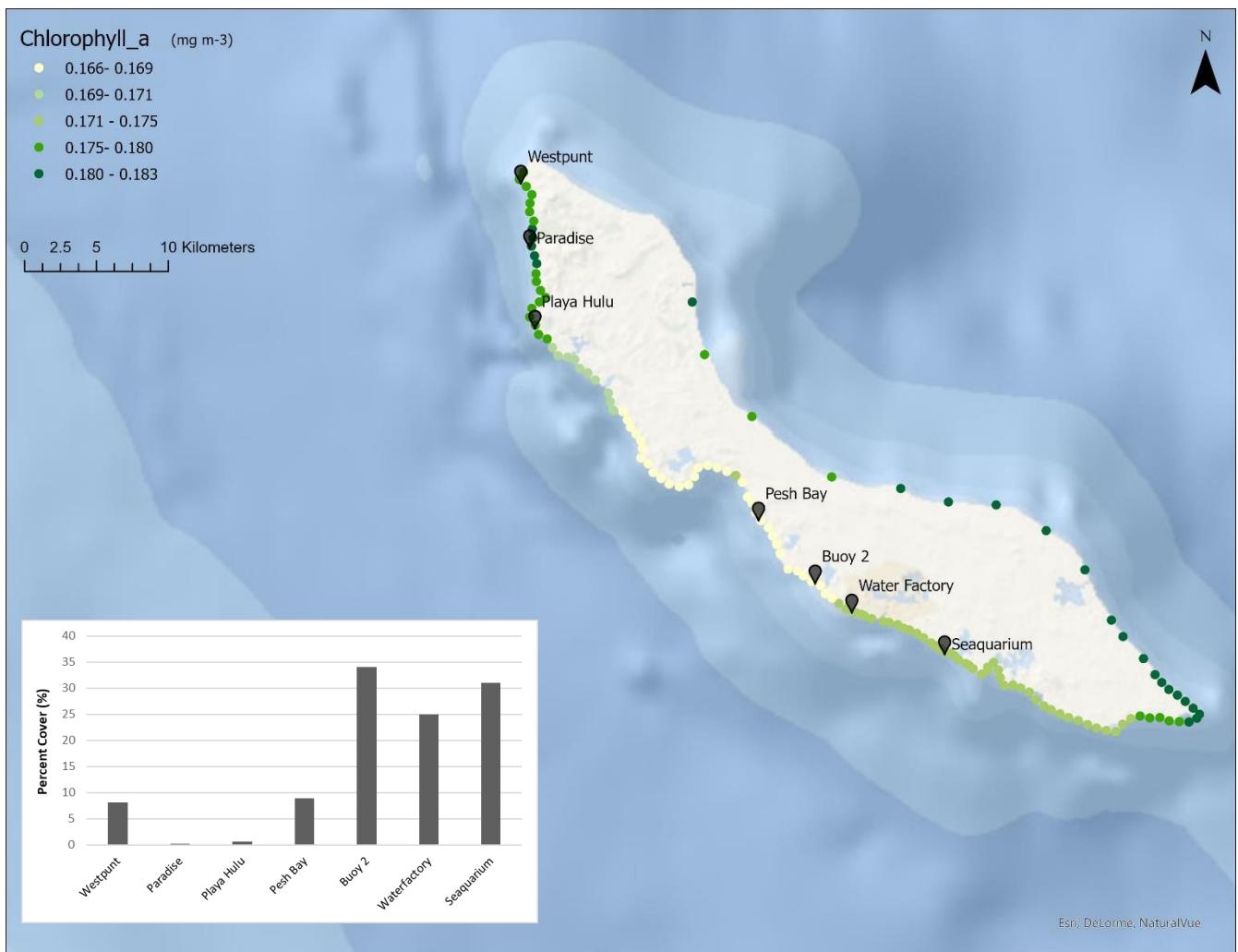
Figure 6 Distribution of sites studied and approximate chlorophyll a concentrations. Average percent cover of M. mirabilis *was less in the northwestern sites (average percent cover of* M. mirabilis *ranged from 0.2 – 8% at Westpunt, Paradise and Playa Hulu) where chlorophyll a concentrations were the highest (average chlorophyll a values ranged from 0.17 – 0.18 mg m⁻³).*
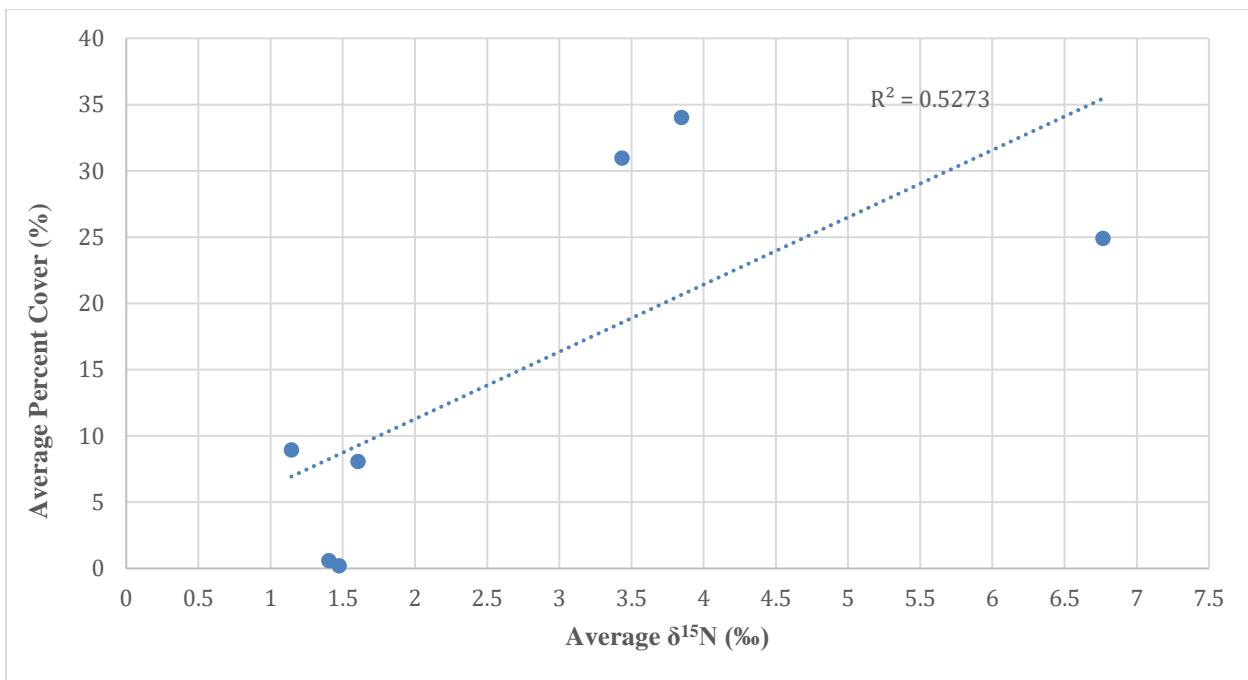
Figure 7 Average δ15N (‰) and percent Cover (%) of M. mirabilis *A linear regression revealed a positive relationship between the average percent cover of M. mirabilis and anthropogenic derived nitrogen (δ15N).* $R^2 = 0.52$, *p value = 0.064.*
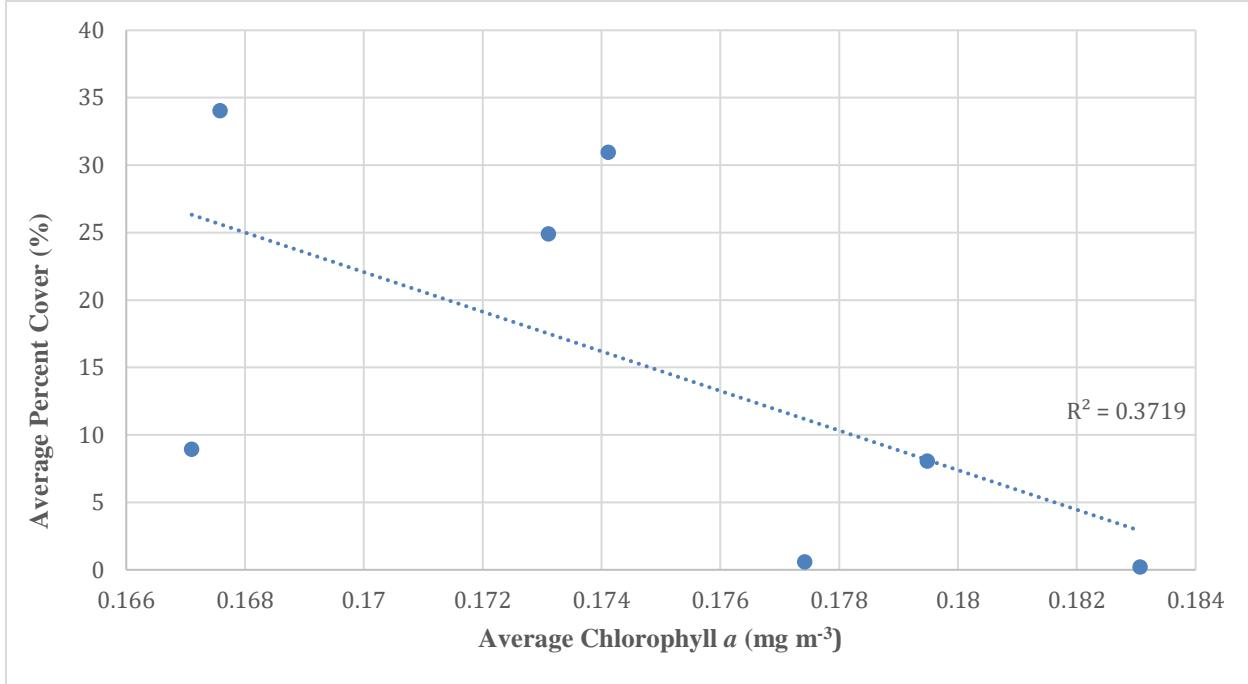
Figure 8 Average chlorophyll a (mg m-3) and percent Cover (%) of M. mirabilis. *A linear regression revealed a weak negative relationship between the average percent cover of M. mirabilis and concentrations of Chlorophyll a (mg m-3). R2 = 0.37, p value = 0.145*

Four out of the seven sites showed an increase in cover of *M. mirabilis* from 2016 to 2020, while the remaining three showed a decrease in cover from 2016 to 2020. Westpunt, Paradise, Water Factory and Seaquarium increased in cover (10-26% increase) and Playa Hulu, Pesh Bay, and Buoy 2 decreased in cover (1-12 % decrease) (*See Table 2*).

Linear regressions were performed for individual sites to examine whether there was a significant change (i.e. appreciable difference) in growth through time. The dependent variable was growth characterized as change in percent cover; the independent variable was time measured from 2016 to 2020, with the null hypothesis that the growth of *M. mirabilis* is not significant through time. Results from the linear regressions were used to discern whether the growth of *M. mirabilis* followed a significant positive or negative trend from 2016 to 2020.

It was found that the site Seaquarium experienced significant growth from 2016 to 2020 ($R^2 = 0.8201$, p value $= 0.0342$) (See *Figure 9*). Water Factory and Westpunt experienced moderate significance for growth from 2016 to 2020 (Water Factory $R^2 = 0.6815$, p value $= 0.0851$, Westpunt $R^2 = 0.6781$, p value $= 0.0866$) (See *Figure 9*).

The remaining sites, Buoy 2, Pesh Bay, Playa Hulu, and Paradise, showed no statistical significance that there was a significant change in growth over the five time points from 2016 to 2020 (See *Figure 9*). However, the growth of *M. mirabilis* at Buoy 2, Pesh Bay, and Playa Hulu showed negative growth from 2016 to 2020 despite being statistically insignificant in the linear regression (*See Table 2*). Paradise showed little change in percent cover from 2016 to 2020 in the linear regression (See *Figure 9)* despite showing a 10% change in cover from 2016 to 2020 (*See Table 2*).

Table 2 Average percent cover and change in average percent cover from 2016 to 2020.

| Site (North to South)	Average Cover (%) in 2016	Average Cover (%) in 2020	Percent Change from 2016- 2020
Westpunt	6.6	8.4	26.0%
Paradise	0.1	0.2	10.9%
Playa Hulu	0.7	0.6	-11.9%
Pesh Bay	9.9	9.1	-8.0%
Buoy 2	33.8	33.2	-1.7%
Water Factory	21.4	26.8	25.1%
Seaquarium	27.8	34.8	25.3%
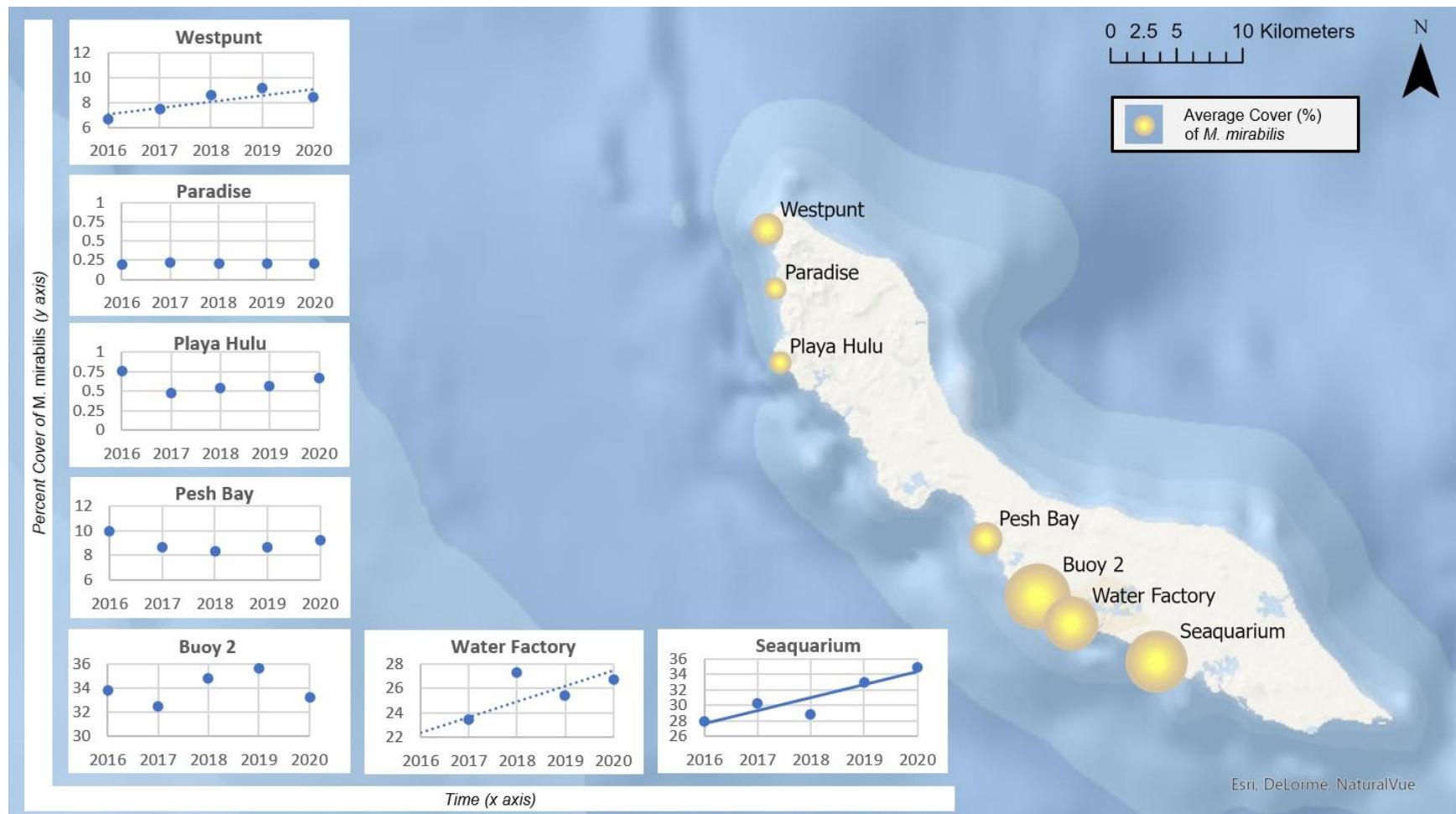
Figure 9 Average percent cover, growth, and linear regressions for each site. Dotted trend lines for Westpunt and Water Factory represent moderate significance that there was an appreciable difference in the growth of M. mirabilis *from 2016 to 2020 (Westpunt $R^2 = 0.67$, p value = 0.086, Water Factory ($R^2 = 0.68$, p value = 0.085). The solid trendline for Seaquarium represents there was statistical significance that there was an appreciable difference in growth from 2016 to 2020 ($R^2 = 0.82$, p value = 0.034).*

Table 3 Average percent cover of M. mirabilis*, percent change in cover, and average nitrogen and chlorophyll a values for each site.*

Sites (North to South)	Average Cover (%) 2016-2020	Change in Cover (%) 2016-2020	Average $\delta^{15}N$ (‰)	Average Chlor a (mg m^{-3})
Westpunt	8.1 %	26.0%	1.61	0.179
Paradise	0.2 %	11.0%	1.47	0.183
Playa Hulu	0.6 %	-11.9%	1.40	0.177
Pesh Bay	8.9 %	-8.0%	1.14	0.167
Buoy 2	34.0 %	-1.8%	3.85	0.168
Water Factory	24.9 %	25.1%	6.77	0.173
Seaquarium	31.0 %	25.3%	3.43	0.174

Discussion

Prior to beginning this study, anecdotal evidence pointed to higher percent cover of *M. mirabilis* in areas proximal to higher nutrient loads. However, it was hypothesized that the percent cover and growth of *M. mirabilis* would be highest among both nutrient gradients, of chlorophyll *a* and $\delta^{15}N$, in response to resource availability.

Considering the many detrimental effects that anthropogenic nutrient loading can have on coral reefs, our results were surprising. It was unexpected to find the highest average percent cover and the most significant growth rates of *M. mirabilis* in the sites with the highest exposure to anthropogenic nutrient loading, rather than the areas with naturally occurring nutrients and less human impact.

All three of the sites in the south with the highest anthropogenic nutrient loads ($\delta^{15}N$) (Seaquarium, Water Factory, and Buoy 2) had the highest average percent cover of *M. mirabilis* in comparison to the other four sites (Pesh Bay, Playa Hulu, Paradise, and Westpunt) (*See Table 3*). The percent cover and growth increased from 2016 to 2020 in two of these sites (Water Factory and Seaquarium) with some of the highest exposure to anthropogenic nutrient loads. Buoy 2 had the second highest $\delta^{15}N$ values and showed an increase in cover from 2017 to 2019, with a slight decrease in 2020, while the average percent cover from 2016 to 2020 was the highest of all the sites (34%).

We expected to find equivalent growth rates and percent cover of *M. mirabilis* in regions with naturally occurring nutrients and less anthropogenic impacts. Our results negated this hypothesis. The sites with the lowest percent cover of *M. mirabilis* (Westpunt, Paradise, and Playa Hulu) were located on the northwestern portion of the leeward reef tract where *chlorophyll a* concentrations were the highest and human impacts were the lowest. Chlorophyll *a* concentrations were not drastically different between the sites (average chlorophyll *a* values were between 0.16 and 0.18 mg m^{-3} for all seven sites), which could have impacted the results of this study.

Other considerations that might have impacted the results of this study include the ratio and concentrations of anthropogenic inputs of nutrients at each site. Previous studies have shown that the effects of nutrient loading on coral physiology is likely to depend on the concentration, the type of nutrient present and is often species-specific.[42] Although the $\delta^{15}N$ values in our sites with the highest percent cover *M. mirabilis* were above our parameters used to indicate exposure to anthropogenic nutrient loading ($\delta^{15}N > 1.5$–2 ‰), the concentrations might not have been high enough to be detrimental to *M. mirabilis* ($\delta^{15}N$ averages for these sites ranged from 3 – 6 ‰) (*See*

Table 3). These results coincide with findings from other studies that show moderate nutrient concentrations have positive impacts on the physiology and survivorship of corals with a higher propensity to feed heterotrophically. [8] [41] Furthermore, the presence of other limited nutrients in the water column could have impacted potential negative effects of nutrient enrichment in these sites. For example, the coupling of phosphorus with nitrogen has been found to counteract the negative impacts of thermal stress on corals by maintaining calcification and metabolic rates.[41]

While this study speculates that anthropogenic inputs of nutrients could contribute to food availability for *M. mirabilis*, this can only be confirmed through the stable isotope analysis of colonies found at each site. Future *in situ and ex situ* experiments with *M. mirabilis* should disentangle the uptake rates of different sources and types of nitrogen (inorganic vs organic nitrogen, anthropogenic vs natural) and the physiological effects of nitrogen enrichment on *M. mirabilis* (changes in calcification, tissue growth, thermal tolerance, photosynthetic rates, Symbiodinium density, etc.). Such experiments will improve our understanding of how anthropogenic nutrients affects heterotrophic coral species beyond *M. mirabilis.*

However, our findings make sense in comparison to past studies conducted on the feeding and effects of nitrogen enrichment on *M. mirabilis*. In a study by Maier C, et al., (2010) the growth of *Madracis spp.* was found to be nitrogen-limited in shallow waters (similar to the depths at our study sites), and that heterotrophic feeding in *Madracis spp.* was a response to food availability. [56] A recent study showed that although the uptake rates were low compared to cyanobacteria and turf algae, *M. mirabilis* was found to consume nitrate, ammonium and phosphate from a sediment plume caused by runoff following a large rainstorm event in Curaçao.[57] Pulses of anthropogenic nutrients may serve as an available food source for *M. mirabilis* in nutrient-limited waters*,* which could contribute to the increased growth and percent cover in the sites most impacted by human activity.

Other observations and directions for future research

Other confounding environmental and biological factors could have contributed to the growth and distribution of *M. mirabilis* across diverse environmental gradients that were not accounted for in this study.

Life History of M. mirabilis
One consideration is how the life history and multi-fate dynamics of *M. mirabilis* might have affected the growth and percent cover calculated from 2016 to 2020. Quantified in the 2019 paper by Brito-Milan et al., large patches of this weedy species often grow exponentially until breaking into many small patches before undergoing rapid fission/fusion. It is unknown if the years observed (2016-2020) were during a cycle of shrinking (large colonies breaking into smaller patches) or rapid growth (fission and fusion of smaller patches), which are independent of nutrient enrichment and resource availability.

Examples of this include Pesh Bay. Although Pesh Bay had the lowest average for percent cover of *M. mirabilis* (8.9%) among the southern sites, it was clear from the imagery that the area likely experienced a recent disturbance or is experiencing a boom-bust cycle of *M. mirabilis*. It could be possible that following the years observed in this study from 2016-2020, the smaller fragmented colonies from the former large patch of *M. mirabilis* may undergo rapid growth through fusion and fission.

Not having a comprehensive understanding of how long these cycles persist and repeat could complement or negate our findings. Future research should look at models following 2020, if available thereafter, to see if and how the growth patterns differ from what our data have shown.

Community Dynamics

Potential declines of other coral taxon at each of these sites could have reduced the competition for space upon these reefs, in which *M. mirabilis*, an opportunistic and weedy species, might have been able to occupy open space as a result. However, this hypothesis does not appear to hold true in sites such as Pesh Bay, which had the fourth lowest average for percent cover of *M. mirabilis* in this study (8.9%) and one of the lowest averages for total percent cover including other coral taxon along the leeward coast (total coral cover for this region was around 7.5% from the 2015 CORE study by Sandin et al.). Average nutrient values were also both low for Pesh Bay (chlorophyll *a* = 0.167 and $\delta^{15}N$ =1.14). As a comparison, Seaquarium had one of the highest averages for percent cover of *M. mirabilis* (average percent cover from 2016 to 2020 was 31%) and one of the highest percentages for total coral cover including other coral taxon (around 22.5 - 37% from the 2015 CORE study by Sandin et al.).[48] It would be worth investigating what percentage of the total coral cover *M. mirabilis* comprises for each of the sites.

Including abundance into a future study could serve as an interesting metric to see how the biodiversity of other coral taxon and benthos has shifted in the sites where there has been the most growth and percent cover of *M. mirabilis*. Observations of other abundant coral taxon could provide insight as to how other species may also be more resilient to environmental stressors, or how they might be in competition for space with *M. mirabilis.*

Wave Exposure as an Environmental Predictor

Although this study focused on nutrient gradients as an environmental predictor of the growth and distribution of *M. mirabilis*, wave exposure was found to be one of the strongest physical environmental variables in predicting the total cover of reef-building benthic assemblages according to the CORE study from 2015.[48] Considering that wave exposure and intensity could affect the flow of nutrients and fragmentation of *M. mirabilis* colonies, wave action should be used in further analysis in identifying the potential effects on the growth, abundance, and distribution of *M. mirabilis*.

Conclusion

The interpretation of our results should not undermine the importance of reducing threats to coral reefs on both local and global levels. While this study could provide some insight as to how *M. mirabilis* might be better adapted to anthropogenic nutrient enrichment, these data are a snapshot of a more dynamic, complex picture. Much is left to learn regarding the effects of resource availability on heterotrophic plasticity and increased tolerance to environmental stressors and shifting oceanic conditions. Further in-depth investigation is needed to explore how other environmental factors are likely to act synergistically to affect the growth and distribution of heterotrophic, opportunistic coral species such as *M. mirabilis* in the Caribbean.

However, we found the highest growth and percent cover of *M. mirabilis* in areas proximal to epicenters of human activity with the worst water quality, perhaps indicative that *M. mirabilis* has a competitive edge in withstanding environmental stressors on both local and global scales. The identification of more resilient, heterotrophic species, including *M. mirabilis,* could provide

resource managers and coral restoration practitioners with information to improve current practices, and valuable insights for the future of Caribbean coral reefs.

Acknowledgements

References

[1] Knowlton N, Grottoli AG, Kleypas J, Obura D, Corcoran E, de Goeij JM, Felis T, Harding S, Mayfield A, Miller M, Osuka K, Peixoto R, Randall CJ, Voolstra CR, Wells S, Wild C, Ferse S. 2021. Rebuilding Coral Reefs: A Decadal Grand Challenge. International Coral Reef Society and Future Earth Coasts 56 pp.

[2] United Nations Environment Programme, Coral Reef Unit. *Coral Reefs - Valuable but Vulnerable*. Retrieved: http://coral.unep.ch/Coral_Reefs.html

[3] Conservation International. 2008. Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation. Center for Applied Biodiversity Science, Conservation International, Arlington, VA, USA.

[4] ResourceWatch. *Coral Reefs: Status and outlook of coral reefs around the world*. Retrieved: https://resourcewatch.org/dashboards/coral-reefs

[5] Jackson, Jeremy & Donovan, Mary & Cramer, Katie & Lam, Vivian. (2014). Status and Trends of Caribbean Coral Reefs: 1970-2012. 10.13140/2.1.4868.6726.

[6] Jeremy B. C. Jackson, Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., & Warner, R. R. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, *293*(5530), 629–638. http://www.jstor.org/stable/3084305

[7] Sturaro, N., Hsieh, Y. E., Chen, Q., Wang, P.-L., & Denis, V. (2021). Trophic plasticity of mixotrophic corals under contrasting environments. *Functional Ecology*, 35, 2841– 2855. https://doi.org/10.1111/1365-2435.13924

[8] Ezzat, L, Maguer, J-F, Grover, R, Rottier, C, Tremblay, P, Ferrier-Pagès, C. Nutrient starvation impairs the trophic plasticity of reef-building corals under ocean warming. *Funct Ecol*. 2019; 33: 643– 653. https://doi.org/10.1111/1365-2435.13285

[9] Fox, Michael & Williams, Gareth & Johnson, Maggie D. & Radice, Veronica & Zgliczynski, Brian & Kelly, Emily & Rohwer, Forest & Sandin, Stuart & Smith, Jennifer. (2018). Gradients in Primary Production Predict Trophic Strategies of Mixotrophic Corals across Spatial Scales. Current Biology. 28. 10.1016/j.cub.2018.08.057.

[10] Grottoli, Andrea & Rodrigues, Lisa & Palardy, James. (2006). Heterotrophic plasticity and resilience in bleached corals. Nature. 440. 1186-9. 10.1038/nature04565.

[11] Towle, E. K., Enochs, I. C., & Langdon, C. (2015). Threatened Caribbean coral is able to mitigate the adverse effects of ocean acidification on calcification by increasing feeding rate. *PloS one*, *10*(4), [e0123394]. https://doi.org/10.1371/journal.pone.0123394

[12] Goreau, Thomas & GOREAU, NORA & YONGE, C.. (1971). Reef Corals: Autotrophs or Heterotrophs?. Biological Bulletin. 141. 10.2307/1540115.

[13] Houlbreque, Fanny & Ferrier-Pagès, Christine. (2008). Heterotrophy in Tropical Scleractinian Corals. Biological reviews of the Cambridge Philosophical Society. 84. 1-17. 10.1111/j.1469-185X.2008.00058.x.

[14] Selosse, M.-A., Charpin, M. and Not, F. (2017), Mixotrophy everywhere on land and in water: the grand écart hypothesis. Ecol Lett, 20: 246-263. https://doi.org/10.1111/ele.12714

[15] L. Muscatine, James W. Porter, Reef Corals: Mutualistic Symbioses Adapted to Nutrient-Poor Environments, *BioScience*, Volume 27, Issue 7, July 1977, Pages 454–460, https://doi.org/10.2307/1297526

[16] Odum, H.T. and Odum, E.P. (1955), Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll. Ecological Monographs, 25: 291-320. https://doi.org/10.2307/1943285

[17] L. Muscatine, James W. Porter, Reef Corals: Mutualistic Symbioses Adapted to Nutrient-Poor Environments, *BioScience*, Volume 27, Issue 7, July 1977, Pages 454–460, https://doi.org/10.2307/1297526

[18] A. S. Huffmyer, C. J. Johnson, A. M. Epps, J. D. Lemus, and R. D. Gates, "Feeding and thermal conditioning enhance coral temperature tolerance in juvenile Pocillopora acuta," Royal Society Open Science, vol. 8, no. 5, May 2021.

[19] Anthony KR, Fabricius KE. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol. 2000 Sep 20;252(2):221-253. doi: 10.1016/s0022-0981(00)00237-9. PMID: 10967335.

[20] Ferrier-Pagès, Christine & Witting, Jan & Tambutté, Sylvie & Sebens, Kenneth. (2003). Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral Stylophora pistillata. Coral Reefs. 22. 229-240. 10.1007/s00338-003-0312-7.

[21] Williams, G.J., Sandin, S.A., Zgliczynski, B.J. *et al.* Biophysical drivers of coral trophic depth zonation. *Mar Biol* **165,** 60 (2018). https://doi.org/10.1007/s00227-018-3314-2

[22] Marine Biology, Biol 410. (n.d.). *Marine Biology: Ocean Primary Productivity*. Ocean productivity. Retrieved June 2, 2022, from https://public.wsu.edu/~dybdahl/lec10.html

[23] Gove, J., McManus, M., Neuheimer, A. *et al.* Near-island biological hotspots in barren ocean basins. *Nat Commun* **7,** 10581 (2016). https://doi.org/10.1038/ncomms10581

[24] Sebens, K.P., Vandersall, K.S., Savina, L.A. *et al.* Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. *Mar. Biol.* **127,** 303–317 (1996). https://doi.org/10.1007/BF00942116

[25] Ferrier-Pagès, Christine & Rottier, Cécile & Béraud, Eric & Levy, Oren. (2010). Experimental assessment of the feeding effort of three scleractinian coral species during a thermal stress: Effect on the rates of photosynthesis. Journal of Experimental Marine Biology and Ecology. 390. 118-124. 10.1016/j.jembe.2010.05.007.

[26] Chapron L, Schoepf V, Levas SJ, Aschaffenburg MD, Warner ME and Grottoli AG (2022) Natural Variability in Caribbean Coral Physiology and Implications for Coral Bleaching Resilience. Front. Mar. Sci. 8:811055.doi: 10.3389/fmars. 2021. 811055

[27] Britannica, T. Editors of Encyclopaedia (2019, April 10). *Curaçao. Encyclopedia Britannica*. https://www.britannica.com/place/Curacao

[28] Vermeij MJA (2012) The Current State of Curaçao's Coral Reefs. Carmabi Foundation and University of Amsterdam. 34 p.

[29] Sandin, Stuart & Sampayo, Eugenia & Vermeij, Mark. (2008). Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. Caribbean Journal of Science. 44. 10.18475/cjos.v44i2.a2.

[30] Estep, A., Sandin, S., & Vermeij, M. (2017). (rep.). *The State of Curaçao's Coral Reefs* (pp. 8–37). Waitt Institute.

[31] de Bakker, Didier & Meesters, Erik & Bak, Rolf & Nieuwland, Gerard & Duyl, Fleur. (2017). Long-term Shifts in Coral Communities On Shallow to Deep Reef Slopes of Curaçao and Bonaire: Are There Any Winners?. Frontiers in Marine Science. 4.

[32] Brito-Millán, Marlene & Vermeij, Mark & Alcantar, Esmeralda & Sandin, Stuart. (2019). Coral reef assessments based on cover alone mask active dynamics of coral communities. Marine Ecology Progress Series. 630. 55-68. 10.3354/meps13128_.

[33] Sebens, K.P. & Grace S. P & Helmuth, B. & Maney Jr, E. J. & Miles, J. S. (1998). Water flow and prey capture by three scleractinian corals, *Madracis mirabilis, Montastrea cavernosa* and *Porites porites*,

[34] Bak, R. & Joenje, M. & I, Jong & Lambrechts, D. & Nieuwland, Gerard. (1998). Bacterial suspension feeding by coral reef benthic organisms. Marine Ecology-progress Series - MAR ECOL-PROGR SER. 175. 285-288. 10.3354/meps175285.

[35] Heikoop, J.M. & Risk, Michael & Lazier, A.V. & Edinger, Evan & Jompa, Jamaluddin & Limmon, Gino & Dunn, Jennifer & Browne, David & Schwarcz, Henry. (2000). Nitrogen-15 Signals of Anthropogenic Nutrient Loading in Reef Corals. Marine Pollution Bulletin. 40. 628-636. 10.1016/S0025-326X(00)00006-0.

[36] D'Angelo, C., & Wiedenmann, J. (2014). Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Current Opinion in Environmental Sustainability, 7, 82-93.

[37] Szmant, Alina. (2002). Nutrient Enrichment on Coral Reefs: Is It a Major Cause of Coral Reef Decline?. Estuaries. 25. 10.1007/BF02804903.

[38] McCook, L. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* **18,** 357–367 (1999). https://doi.org/10.1007/s003380050213

[39] Hughes, Terence & Rodrigues, Maria & Bellwood, David & Ceccarelli, Daniela & Hoegh-Guldberg, Ove & McCook, Laurence & Moltschaniwskyj, Natalie & Pratchett, Morgan & Steneck, Robert & Willis, Bette. (2007). Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Current biology : CB. 17. 360-5. 10.1016/j.cub.2006.12.049.

[40] Becker, D.M., Putnam, H.M., Burkepile, D.E. et al. Chronic low-level nutrient enrichment benefits coral thermal performance in a fore reef habitat. Coral Reefs 40, 1637–1655 (2021). https://doi.org/10.1007/s00338-021-02138-2

[41] Ezzat, L., Towle, E., Irisson, J.-O., Langdon, C. and Ferrier-Pagès, C. (2016), The relationship between heterotrophic feeding and inorganic nutrient availability in the scleractinian coral *T. reniformis* under a short-term temperature increase. Limnol. Oceanogr., 61: 89-102. https://doi.org/10.1002/lno.10200

[42] K. Koop, D. Booth, A. Broadbent, J. Brodie, D. Bucher, D. Capone, J. Coll, W. Dennison, M. Erdmann, P. Harrison, O. Hoegh-Guldberg, P. Hutchings, G.B. Jones, A.W.D. Larkum, J. O'Neil, A. Steven, E. Tentori, S. Ward, J. Williamson, D. Yellowlees, ENCORE: The Effect of Nutrient Enrichment on Coral Reefs. Synthesis of Results and Conclusions, Marine Pollution Bulletin, Volume 42, Issue 2, 2001, Pages 91-120, ISSN 0025-326X, https://doi.org/10.1016/S0025-326X(00)00181-8.

[43] Dailer ML, Knox RS, Smith JE, Napier M, Smith CM. Using delta 15N values in algal tissue to map locations and potential sources of anthropogenic nutrient inputs on the island of Maui, Hawai'i, USA. Mar Pollut Bull. 2010 May;60(5):655-71. doi: 10.1016/j.marpolbul.2009.12.021. Epub 2010 Jan 12. PMID: 20070989.

[44] Duyl, Fleur. (1985). Atlas of the living reefs of Curaçao and Bonaire (Netherlands Antilles) /. Studies of Flora and Fauna of Surinam and the Netherlands Antilles. 117. 1-37 plus maps.

[45] Dutch Caribbean Nature Alliance. (2017). Status of Curaçao's Reefs (Report No. 4). BioNews. http://www.dcnanature.org/wp-content/uploads/2017/10/BioNews-2017-4-Status-Curacao-Reef.pdf.

[46] Edwards, C.B., Eynaud, Y., Williams, G.J. et al. Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. Coral Reefs 36, 1291–1305 (2017). https://doi.org/10.1007/s00338-017-1624-3

[47] Kodera, S. M., Edwards, C. B., Petrovic, V., Pedersen, N. E., Eynaud, Y., and Sandin, S. A. (2020). Quantifying life history demographics of the scleractinian coral genus Pocillopora at Palmyra Atoll. Coral Reefs 39, 1091–1105. doi: 10.1007/s00338-020-01940-8

[48] Sandin, S.A., Alcantar, E., Clark, R., de Leon, R., Dilrosun, F., Edwards C.B., Estep A.J., Eynaud, Y., French, B.J., Fox, M.D., Grenda, D., Hamilton, S.L., Kramp, H., Marhaver, K.L., Miller, S.D., Roach, T.N.F., Gisette, S., Silveira, C.B., Smith, J.E., Zgliczynski, B.J., & Vermeij, M.J.A. (2015) (in press). *Benthic assemblages are more predictable than fish assemblages at an island scale*.

[49] Lapointe, Brian & Barile, Peter & Matzie, William. (2004). Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys. Journal of Experimental Marine Biology and Ecology. 308. 23-58. 10.1016/j.jembe.2004.01.019.

[50] 100 Island Challenge. (2019). The Scripps Oceanography 100 Island Challenge: Developing conservation targets for coral reefs globally. Retrieved from: http://crc.reefresilience.org/wp-content/uploads/2019/07/SIO_Mosaic_SOP_V3_SingleRig_20190320.pdf

[51] Marre, G., Holon, F., Luque, S., Boissery, P., & Deter, J. (2019). Monitoring Marine Habitats With Photogrammetry: A Cost-Effective, Accurate, Precise and High-Resolution Reconstruction Method. *Frontiers in Marine Science*.

[52] Couch, C. S., Oliver, T. A., Suka, R., Lamirand, M., Asbury, M., Amir, C., Vargas-Ángel, B., Winston, M., Huntington, B., Lichowski, F., Halperin, A., Gray, A., Garriques, J., & Samson, J. (2021). Comparing coral colony surveys from in-water observations and structure-from-motion imagery shows low methodological bias. Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2021.647943

[53] The Cultural Heritage Engineering Initiative (CHEI). (2019). Viscore. The Cultural Heritage Engineering Initiative (CHEI). Retrieved from https://chei.ucsd.edu/viscore/

[54] Sandin Lab, Scripps Institution of Oceanography. (2021). Guide to Viscore. Standard Operating Procedure, unpublished internal document.

[55] Pavoni, G., M. Corsini, M. Callieri, G. Fiameni, C.B. Edwards and P. Cignoni. 2020. On improving the training of models for the semantic segmentation of benthic communities from orthographic imagery. Remote Sensing. DOI: 10.3390/rs12183106

[56] Maier C, Weinbauer MG, Pätzold J (2010) Stable isotopes reveal limitations in C and N assimilation in the Caribbean reef corals *Madracis auretenra*, *M. carmabi* and *M. formosa*. Mar Ecol Prog Ser 412:103-112. https://doi.org/10.3354/meps08674

[57] den Haan, J., Huisman, J., Brocke, H. et al. Nitrogen and phosphorus uptake rates of different species from a coral reef community after a nutrient pulse. Sci Rep 6, 28821 (2016). https://doi.org/10.1038/srep28821