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This Master's Project

Impacts of Nitrogen Enrichment on Corals – A Remote Sensing Approach

By

David E. Carrasco Rivera

is submitted in partial fulfillment of the requirements
for the degree of

Master of Science

in

Environmental Management

at the

University of San Francisco

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ABSTRACT

Anthropogenic activities have resulted in ever-increasing threats to coral reefs globally, wherein the rate of environmental changes have exceeded the historical capacity of corals to adapt. This has threatened the persistence of coral ecosystems and their associated ecosystem services, which billions of people rely on for their livelihoods. The most prevalent stressor is nitrogen enrichment, which while present naturally, is exacerbated by the anthropogenic input of nutrients via the discharge of agricultural and urban waste waters. The focus is to answer the central research question of how nitrogen enrichment impacts corals, and how it interacts with other stressors with particular focus on the Caribbean Sea. Nitrogen enrichment directly impacts corals by promoting algae dominance of coral ecosystems, disrupting coral symbiotic relationships, increasing disease prevalence, and indirectly by creating hypoxic conditions and affecting coral calcification rates. The case study of the PNN Los Corales del Rosario y San Bernardo served to demonstrate the use of remote sensing for monitoring chlorophyll-a concentrations and sea surface temperatures, where these two water quality parameters were negatively correlated from 2003 to 2021. Promoting the use of these tools is of crucial importance in the Caribbean region, where many local communities lack accessible resources available for environmental management. It is evident that, in addition to reducing nitrogen enrichment events, managers need to implement coordinated management to reduce multiple environmental stressors that affects corals. Finally, it is necessary to provide education that allows local communities to not only identify the challenges that corals face but also the solutions moving forward.

1. INTRODUCTION

1.1 Importance of coral habitats and associated challenges

Despite covering only about 0.5% of the ocean floor, coral reefs are among the most biodiverse natural ecosystems in the world sustaining around 35% of all marine species (Knowlton et al., 2010). This diversity allows coral assemblages to provide various ecological services that bring many benefits to human communities (Buke & Maidens, 2005; UNEP et al., 2018; Zhao et al., 2021). Many of these ecosystem services can translate into socio-economic values. Across the world, these benefits are essential to communities in over 100 countries due to food availability, tourism and recreation, as well as coastal protection (Buke & Maidens, 2005; UNEP et al., 2018; Zhao et al., 2021). Globally, services provided by these ecosystems are estimated to be worth roughly between \$375 billion and \$9.9 trillion per year - all economic values given in US dollars (Zhao et al., 2021). However, due to the increasing threats to coral reefs, and their degraded state, their socio-economic value could drop by between 10-20% within the next 10-20 years, inferring the loss of their ecosystem services (Burke and Maidens, 2005; UNEP et al., 2018).

Regardless of their known ecological services and socio-economic values, coral habitats have faced constantly increasing threats and stressors driven by anthropogenic action over recent decades (Hughes et al., 2003; Nelson & Altieri, 2019; Zhao et al., 2021). These stressors have resulted in more frequent and severe bleaching events, leading corals to lose their microalgae endosymbiont and culminate in coral mortality (Cunning & Baker, 2012; Lapointe, Brian et al., 2019; Lesser, 2021). Given the increased frequency of bleaching events, elevated emissions of carbon dioxide (CO₂), ocean acidification (OA) and increasing temperatures have been considered the most impactful anthropogenic stressor on coral habitats. However, novel research has identified that nutrient enrichment is a major anthropogenic stressor with equally negative or even worsened repercussions (D'Angelo & Wiedenmann, 2014; Lapointe et al., 2019; Zhao et al., 2021). This has been mainly due to the fact that coral reefs have historically prospered in oligotrophic tropical waters, meaning that corals, the main structure-building organisms of these reefs, have adapted to low nutrient concentrations in the water column (D'Angelo & Wiedenmann, 2014; Marubini & Davies, 1996; Zhao et al., 2021).

These oligotrophic conditions of the surrounding environment have been heavily impacted by elevated concentrations of nutrients, also referred to as eutrophication events (Cunning & Baker, 2012; D'Angelo & Wiedenmann, 2014; Lapointe et al., 2019). Though many nutrients play a role in these episodes, elevated nitrogen concentrations in particular have become the most relevant and concerning factor of nutrient enrichment in the field of environmental management. This is mainly due to the vast detrimental impacts of nitrogen enrichment on coral health and dynamics (D'Angelo & Wiedenmann, 2014; Hughes et al., 2003; Zhao et al., 2021). It has been identified that nitrogen enrichment reduces coral health in various direct and indirect ways. Firstly, nitrogen enrichment directly affects coral health by promoting primary productivity resulting in excess macroalgae cover, disrupting strictly necessary coral symbiotic relationship with zooxanthellae, and increased prevalence of coral diseases (De'ath & Fabricius, 2010; Vega et al., 2014; Wooldridge, 2020; Zhao et al., 2021). Additionally, indirect impacts of elevated nitrogen concentrations on coral health include the impairment of coral skeletogenesis and the creation of hypoxic zones (Nelson & Altieri, 2019; Webb et al., 2021; Zhao et al., 2021).

To monitor the direct and indirect impacts of nitrogen enrichment on coral ecosystems, field sampling has been the most used methodology. However, due to lack of resources, elevated costs and time consumption, as well as reduced area that can be surveyed and accessed with field sampling, remote sensing tools have emerged as an important tool to tackle some of these challenges (Dodge et al., 1982; Miller & Müller, 1999). Not only is remote sensing data oftentimes free of access, but it can also be performed at large scale and help to monitor areas where physical access is limited (Hochberg, 2010; Hedley et al., 2016). Promoting the use of these tools is of crucial importance in the Caribbean region, where many local communities not only lack resources, but also have limited access to education and information. Additionally, this region has become a hotspot of nitrogen enrichment as human populations and pressure on the land are continuously increasing.

1.2 Research questions and sub-questions

With the motivation presented above, I formulated a series of research questions and sub-questions to evaluate the different impacts of nitrogen enrichment on coral health. Additionally, I evaluated how nitrogen enrichment interacts with other environmental stressors and the respective consequences on coral colonies. Finally, I also described how remote sensing can help environmental managers to design effective management strategies. The research question and sub-questions are as follows:

1. How does nitrogen enrichment influence coral health and the environmental conditions that corals face?

1.1 How does nitrogen enrichment influence the overgrowth of macroalgae over coral habitats?

1.2 How does nitrogen enrichment influence the obligatory symbiotic relationship between coral and microalgae?

1.3 How does nitrogen enrichment influence the prevalence and severity of coral diseases?

1.4 How does nitrogen enrichment influence coral calcification processes?

1.5 How does nitrogen enrichment influence oxygen availability in coral habitats?

2. How does nitrogen enrichment interact with other anthropogenically-induced environmental stressors and what are the impacts to coral colonies?

2.1 How does overfishing pressure on coral ecosystems interact with nitrogen enrichment and what are the consequences for corals?

2.2 How does increasing temperature on coral ecosystems interact with nitrogen enrichment and what are the consequences for corals?

2.3 How does ocean acidification on coral ecosystems interact with nitrogen enrichment and what are the consequences for corals?

3. How can remote sensing be applied to monitor the impacts of nitrogen enrichment on coral habitats?

3.1 What are some of the applications of remote sensing for monitoring coral ecosystems?

3.2 What are some of the challenges when applying remote sensing to coral habitats?

4. After conducting the respective comparative literature review, I applied these concepts to a case study region to evaluate how chlorophyll-a (Chl-a) concentrations and sea surface temperatures (SST) have changed in the Parque Nacional Natural Los Corales del Rosario y San Bernardo in Colombia, from 2003 to 2021. This would enable to see the applicability of remote sensing on water quality parameters for coral habitats and find some relationship with adjacent land practices. Additionally, this would allow me to find relationships between driver of nutrient enrichment, such as terrestrial land use activities, and the concentrations of Chl-a in the region.

2. BACKGROUND

2.1 Ecological dynamics

To understand the different mechanisms by which nitrogen enrichment impacts coral health and the conditions they face, it is important to understand various ecological dynamics that occur in coral ecosystems. For the purpose of this study, the three ecological dynamics that are going to be examined include primary productivity in coral habitats, the strictly necessary symbiotic relationship of corals with zooxanthellae microalgae, coral diseases, and oxygen availability in these ecosystems.

Firstly, given the oligotrophic characteristics of the water column, primary productivity is relatively low in these habitats (Bell, Peter et al., 2014; Zhao et al., 2021). This means that the presence of marine vegetation is traditionally restricted in these waters where nutrients are a limiting factor. Particularly, nitrogen has historically been identified as the most common limiting factor for marine vegetation growth; because its concentrations are typically very low, it is taken up rapidly by the already present vegetation (D'Angelo & Wiedenmann, 2014;

Lapointe et al., 2019). Most of this naturally available nitrogen comes from nitrogen fixing organisms, ocean upwelling, and atmospheric deposition (Lapointe et al., 2019). However, when nitrogen is deposited in the water from non-natural sources such as human agricultural activity and discharge of waste waters, whereby primary productivity is promoted, resulting in plankton blooms which oftentimes lead to macroalgae blooms (Bell, P., 1992; D'Angelo & Wiedenmann, 2014; Lapointe et al., 2019; Zhao et al., 2021). These increased macroalgae densities act via various mechanisms as stressors to coral assemblages, oftentimes due to competition, which can result in the shift from coral- to aquatic vegetation-dominated ecosystems.

Another relevant ecological process that is crucial to understanding the impacts of nitrogen enrichment on coral health is its repercussions on the coral's strict symbiotic relationships. Although coral colonies thrive under oligotrophic conditions, they have adapted to be amongst the most productive ecosystems in the world (Hughes et al., 2003; UNEP, 2018). This evolutionary adaptation has been favored by the highly specialized and efficient relationship with their microbiome. Particularly, corals have developed a mutualistic symbiotic relationship with zooxanthellae, single-celled dinoflagellate algae from the genus *Symbiodinium* (Figure 1) (Cunning & Baker, 2012; D'Angelo & Wiedenmann, 2014; Dunn et al., 2012). The relationship is purely based on metabolic processes of both organisms. Zooxanthellae photosynthetic processes have many byproducts including calcium ions (Ca^{+2}), fixed carbon (sugars as energy), and oxygen (O_2) which are transferred to the coral host for metabolic purposes via cell membranes (Becker & Silbiger, 2020). The coral host uses these byproducts, particularly Ca^{+2} and fixed carbon for calcification, and O_2 for respiration purposes. These coralline metabolic processes yield CO_2 production, which is then used again by zooxanthellae for photosynthesis, making it a loop of nutrient recycling (Becker & Silbiger, 2020; Wooldridge & Done, 2009). This relationship has shaped scientific understanding of the contradictory surrounding low nutrient concentrations of such rich and highly productivity and biodiverse ecosystems. Said relationship is characterized by maximum efficiency in nutrient absorption and recycling from both the coral and the zooxanthellae (Dunn et al., 2012; Marubini & Davies, 1996).

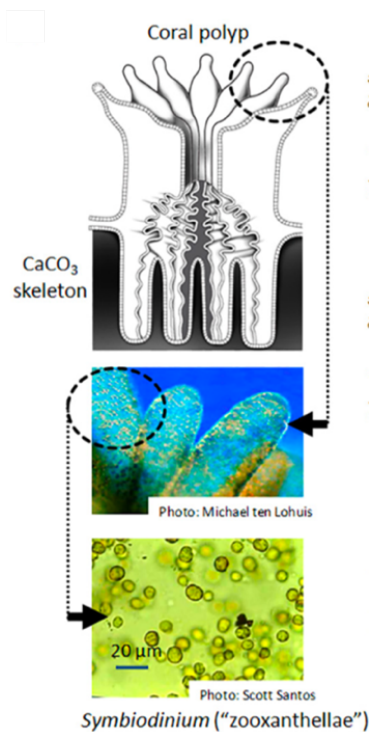


Figure 1. Microscopic view of the location of the endosymbiont zooxanthellae within the tissue of the respective coral host (Wooldridge, 2020).

Efficient nutrient cycling is vital as it is the main way by which corals obtain nutrients to perform calcification processes. Calcification is the process that corals conduct in order to produce their skeleton and be able to grow and expand across their habitats and provide their ecosystem services (Becker & Silbiger, 2020; Dunn et al., 2012). Corals have been described to form their skeleton using aragonite, a calcium-carbonate mineral compound that, as its name indicates, is formed by the combination of calcium (Ca^{+2}) and carbonate (CO_3^{2-}) ions (Silbiger et al., 2018). To conduct calcification, corals obtain calcium and carbon as photosynthetic byproducts from their endosymbionts (Edinger et al., 2000; Webb et al., 2021). However, as a microalgae species, zooxanthellae utilize nitrogen for growth purposes. Therefore, during nitrogen enrichment events, their relationship with corals is oftentimes disturbed rapidly due to increased nitrogen availability. This disruption results in the expulsion of the algal endosymbiont from the coral host, or by the abandonment of the zooxanthellae away from the

coral, which leads to coral starvation and, very frequently, to eventual coral mortality (Cunning & Baker, 2012).

Nitrogen enrichment not only affects the microbiome by disrupting coral-zooxanthellae relationship, but it can also increase frequency and severity of coral diseases. Diseases are a normal component of ecosystems' ecological processes. In natural habitats, diseases act as a mechanism that regulate population densities, keeping the ecosystem in check, which guarantees that resources are still being utilized at a sustainable rate (Bruno et al., 2003; Kuta & Richardson, 2002). In coral assemblages, given the oligotrophic conditions of the water column, it is relatively easy for corals and symbiotic zooxanthellae to deplete the already limited resources. However, diseases such as the black-band disease (BBD), white syndrome disease (WSD), yellow-band disease, and aspergillosis among others, regulate the over-colonization of coral assemblages across marine environments (Baker et al., 2007; Kuta & Richardson, 2002; Redding et al., 2013). Though these diseases are a normal part of coral ecosystem processes, in recent decades, coral diseases have experienced an exponential increase. This increase in disease prevalence has not only been described in frequency of occurrence, but also in higher severity, elevating tissue mortality rates in coral colonies at a pace faster than corals can recover (Baker et al., 2007; Bruno et al., 2003; Redding et al., 2013; Vega et al., 2014). Though there are various factors that affect this increase in coral diseases, anthropogenic activities have been identified as the most prominent causes. Nutrient enrichment, particularly elevated nitrogen concentrations in the water column, has shown to have a direct impact in the prevalence of coral disease outbreaks. These negative effects occur either by infection of the coral host or by damage to the zooxanthellae endosymbiont (Redding et al., 2013).

Finally, another impact of nitrogen enrichment to coral dynamics is the reduction in the availability of dissolved oxygen (DO). Oxygen levels are a crucial environmental characteristic of marine ecosystems. In coral reefs, oxygen is utilized by most species that inhabit these ecosystems including corals, and it is produced by organisms such as symbiotic zooxanthellae, algal species, and other photosynthetic organisms (Johnson et al., 2021; Nelson & Altieri, 2019). However, oxygen concentrations can fluctuate due to various factors such as seasonality, varied watershed discharge, rain events, and nutrient enrichment among others (Lapointe & Clark,

1992; Nelson & Altieri, 2019). It has been globally accepted that oxygen levels between 2.8mgO₂ and 6.8mgO₂, at 27°C, are considered normal oxygen levels, describing a normoxic environment (Johnson et al., 2021; Nelson & Altieri, 2019). However, when oxygen concentrations fall below 2.8mgO₂ thresholds, the ecosystem is considered hypoxic, oftentimes leading to eventual anoxic conditions, where oxygen levels are completely depleted, and the environment could potentially become a dead zone (Nelson & Altieri, 2019). The development of hypoxic conditions and dead zones in tropical coral ecosystems has recently become a concern for environmental managers. These conditions have been strongly linked to episodes of nitrogen enrichment, particularly in regions such as the Caribbean Sea (Johnson et al., 2021; Lapointe & Clark, 1992; Lapointe, B. & Matzie, 1996; van Tussenbroek et al., 2017).

2.2 Region of interest

The Caribbean Sea is a tropical region that is home to vast coral assemblages, which allows countries in the region to obtain major socio-economic benefits from these ecosystems. In the Caribbean region, every square-kilometer of coral reef approximately contributes between \$100,000 to \$600,000 annually to each country's economy (Burke and Maidens, 2005). Such values have allowed coral reefs in the region to provide approximately \$1.9 billions to fisheries, \$25.5 billions to the tourism and recreation sector, and \$2.2 billions in coastal protection annually (Burke and Maidens, 2005). For example, in the case of the Mesoamerican reef, the largest coral reef system in the Western hemisphere, it is estimated that its ecosystem services will provide at least \$34.6 billions between 2017 and 2030 (UNEP et al., 2018). However, many of these ecosystem have experienced increasing challenges including more frequent nutrient enrichment events, overfishing pressure, raising temperatures, and OA, among others (Burke et al., 2011; UNEP et al., 2018). Moreover, due to rapidly increasing human populations in the region, these impacts continue to aggravate. Particularly, nitrogen enrichment is of special concern in the region due to increasing urban development, agricultural and grazing pressure on the land, and deforestation events (Burke et al., 2011; Hedley et al., 2016; UNEP et al., 2018). Currently, most of the known reefs in the region are threatened at some level by these human activities (Figure 2 – Burke et al., 2011).



Figure 2. Reefs at risk in the Caribbean Sea due to anthropogenic activities (Burke et al., 2011).

2.3 The basics of remote sensing

To understand how remote sensing can be applied to monitor coral habitats, it is necessary to understand what remote sensing is and how it can be used. Remote sensing is defined as the ability to collect data about an object or area at a distance with the use of a device that records information (Cracknell, 2007). By this definition, for example, a photograph is remote sensed data, and the respective data collecting device is the camera. To understand remote sensed data acquisition, it is important to understand wavelength and frequency, electromagnetic spectrum, how this applies to remote sensors, and the resulting spatial resolution. Firstly, it is known that wavelength (measured in nm or μm) and frequency (measured in hertz, Hz.) are components of light. These are respectively defined by light oscillation and its corresponding crest to crest distance, and the frequency of its cycle (Figure 3) (Campbell & Wynne, 2011).

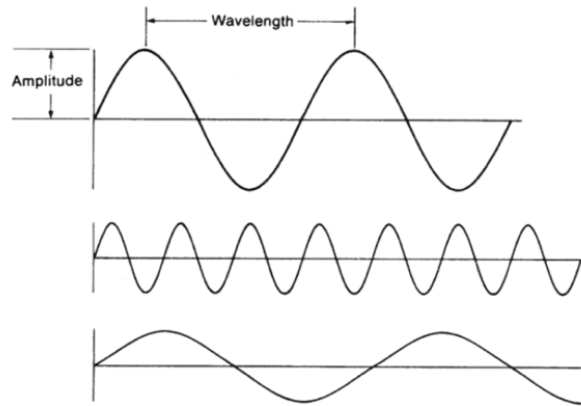


Figure 3. Wavelength, amplitude, and frequency. The first graph graphically defines wavelength. The second graph displays high frequency and short wavelength. Finally, the third graph displays low frequency and long wavelength (Campbell & Wynne, 2011).

These components of light, namely wavelength and frequency, are known to shape the electromagnetic spectrum, which includes ranges such as visible light, ultraviolet, infrared, microwaves, and x-ray among others (Figure 4). For remote sensing, the sensors capture the light that is reflected (radiation) by the surface of the object or area of interest, which most commonly focuses on the wavelength rather than the frequency (Butler et al., 1988). The spectra that are of most useful to remote sensors include ultraviolet range (wavelength of 0.3 to 0.4 μm), visible range (0.4 to 0.7 μm), near infrared (NI) range (0.7 to 3 μm), middle infrared range (3 to 8 μm), and the far infrared range (8 to 1000 μm) among others (Butler et al., 1988; Hochberg, Eric J., 2010).

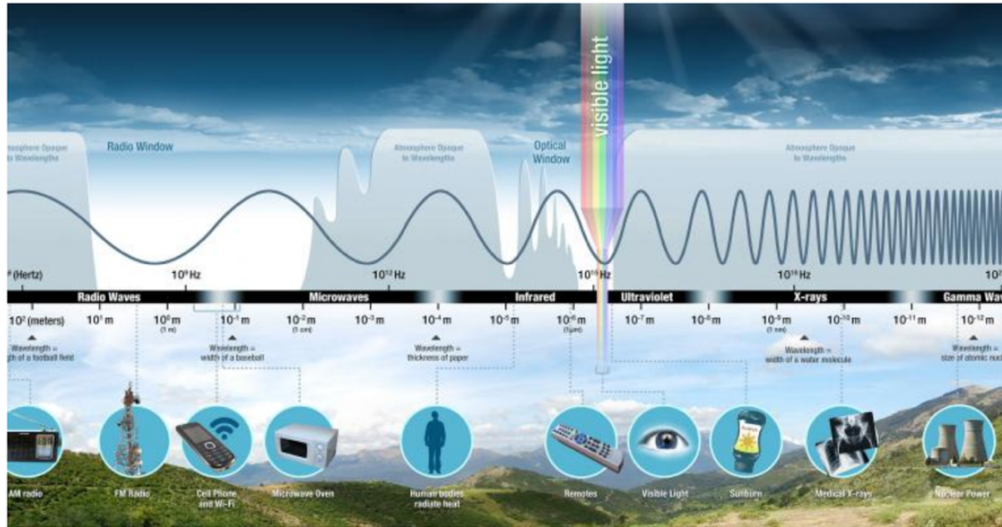


Figure 4. The electromagnetic spectrum, including the wavelength and frequency of some of the categories (Credit to NASA SCIENCE from the website: https://science.nasa.gov/ems/01_intro).

For a recording device to be able to collect the data described above, the two essential components are light sources, and the reflecting surface (Cracknell, 2007). This has yielded to two types of remote sensors: active and passive sensors (Campbell & Wynne, 2011). Active sensors are able to provide their own light, which is then reflected back by the object of interest into the recording device. On the other hand, passive sensors are characterized by detecting natural light that is either emitted or reflected by the object or area of interest. In most cases, reflection of sunlight is the source of light that is reflected to and recorded by this type of sensors, which includes satellites as the most commonly used passive sensors (Figure 5) (Campbell & Wynne, 2011; Cracknell, 2007). Once the sensor has collected the data, it can provide information in the form of pixels. The size of these pixels is defined by the ability of the sensor to receive radiation and relate it to the actual size of the surface area where the radiation originated. This ability is known as spatial resolution, usually measured in factors of meters such as centimeters, meters, and kilometers. Herein, higher resolution covers smaller surface areas (e.g., 1m x 1m resolution), and lower resolution represents larger surface areas (e.g., 50km x 50km resolution) (Butler et al., 1988; Campbell & Wynne, 2011; Cracknell, 2007).



Figure 5. Types of remote sensors. Passive sensors capture reflection of natural light from the object or area of interest. Active sensors provide their own source of light and detect the reflection from the object or area of interest (Credit to NASA Earth Data from the website: <https://earthdata.nasa.gov/learn/remote-sensors>).

Although the imagery acquired via remote sensing can be interpreted in various ways, scientists have to perform classification in order to assign empirical values to the pixels that the sensors provide. There are two types of classification: unsupervised, and supervised classification (Cracknell, 2007). Unsupervised classification is automated and performed by the computer, which assigns statistically similar pixels to respective classes, dividing the dataset in what is described as *natural clusters*. On the other hand, supervised classification is performed by using *training data*. This data is a group of pixels for which certain characteristics are known. These pixel characteristics are then used by the computer to assign a class to those unknown pixels that are similar to the training samples (Butler et al., 1988; Campbell & Wynne, 2011). Both unsupervised and supervised classification processes may vary depending on the scope of the study.

2.4 Case study

To provide an example of how to apply remote sensing for monitoring ecosystem dynamics in coral habitats in the Caribbean Sea, I evaluated the changes of Chl-a concentrations and SST from 2003 to 2021 at the Parque Nacional Natural (PNN) Los Corales del Rosario y San Bernardo in Colombia (Figure 6). Examining Chl-a concentrations would allow for the identification of potential nitrogen enrichment in the area. Additionally, obtaining SST changes

in the region would allow for the understanding of additional relationships between nitrogen enrichment and changing temperatures. I chose this natural park because this geographic region is a protected area in the Colombian Caribbean Sea that is home to historical coral assemblages.



Figure 6. Map of the area of interest for the case study. This map shows the location of the Parque Nacional Natural Los Corales del Rosario y San Bernardo in Colombia.

3. METHODOLOGY

3.1 Bibliographic analysis

For the majority of the paper, peer-reviewed published scientific articles were used to conduct a metanalysis of available literature in the field of coral conservation. Initially, using search engines such as Scopus and Google Scholar, I retrieved articles that examined the various impacts of nitrogen enrichment on coral regions across world, using those terms as key words. The next step was to classify the major impacts of nitrogen enrichment into direct or

indirect impacts, which was based on whether each impact was strictly caused by excess nitrogen, or as a result of one or more of the other impacts. Once the major direct and indirect impacts of nitrogen enrichment on coral health were identified, I performed further literature searches adding key words that related to each impact, e.g., “macroalgae cover”, “zooxanthellae”, “coral diseases”, “coral calcification”, and “hypoxia”. This allowed for a more robust analysis of the various impacts of nitrogen enrichment on coral health and the conditions they face.

As I described and evaluated the major impacts of nitrogen enrichment on coral health, I conducted further literature searches to find relationships between eutrophication and other anthropogenic stressors on coral health. This search allowed me to find ways in which other anthropogenic stressor could aggravate the negative impacts of nitrogen enrichment, and *vice-versa*. Firstly, I investigated major anthropogenic impacts on marine ecosystems, targeting coastal waters with known coral habitats. This allowed me to conduct an additional literature searches, adding key words such as “overfishing”, “climate change”, and “ocean acidification”.

In addition to analyzing literature regarding nitrogen enrichment and other anthropogenic stressors, the purpose of this literature analysis was to also evaluate how remote sensing can be used to monitor coral habitats and nitrogen enrichment events. Herein, I expanded my search to focus on remote sensing for coral ecosystems. This allowed me to conduct literature searches using key words such as “remote sensing”, “coral habitats”, and “water quality”. This search yielded resources that enabled me to describe what remote sensing was, as well as the various applications of these tools to characterizing coral habitats and monitoring different water quality parameter for these ecosystems. Additionally, this allowed me to establish the major challenges of these application and what some of the potential solutions could be.

3.2 Case study

Once I had identified the major impacts of nitrogen enrichment, their interactions with other anthropogenic stressors, and how remote sensing could be used to monitor these habitats, I chose to apply these concepts to a region of interest. I started by examining the

available data in Google Earth Engine, a platform that allows for the extraction of satellite data at a global scale. Herein, I chose to use the Moderate Resolution Imaging Spectroradiometer (MODIS), which is a NASA satellite launched in mid-2002 that contains bands that provide already computed Chl-a concentrations and SST globally. This data availability allowed me to extract these parameters and clip them to the polygon of the boundaries of the PNN Los Corales del Rosario y San Bernardo in Colombia, which I obtained from the World Database of Protected Areas (WDPA) – available within GEE as well.

After the data was obtained, I exported the yearly averages, for both Chl-a and SST, from 2003 to 2021 and within the polygon of the region of interest. With these values, I created an excel spreadsheet where I computed a graph to identify the general trends of the parameters during the defined time frame. Additionally, I extracted the Chl-a imagery from GEE as rasters and imported them into ArcGIS Pro, a processing software that allows for the creation of maps among other geospatial products. This allowed me to examine whether there was any visually evident spatial distribution of these concentrations within the region of interest. Finally, the results of this case study were compared to the conducted literature analysis, allowing for the formulation of recommendations for proper management of coral ecosystems, as well as recommendations of how basic remote sensing tools can be implemented upon monitoring and managing these habitats.

4. EVIDENCE

4.1. Direct impacts of nitrogen enrichment on corals

The most critical mechanisms by which nitrogen pollution affects corals are those that have a direct or immediate impact on coral health. These mechanisms include the shift of living coral cover (LCC) to macroalgae cover, the disruption of the strictly necessary relationship of corals with zooxanthellae microalgae, and the increased frequency and severity of coral diseases. Understanding these processes and their repercussions is crucial, not only so that proper treatment and restoration can be implemented but also so that preventive measures can be developed.

4.1.1 Competition with macroalgae

In recent decades, many historical coral habitats have experienced a shift from LCC to macroalgae dominated habitats, which has been influenced heavily by nitrogen enrichment in the water column. Due to the oligotrophic or low nutrient characteristics of the waters of coral habitats, nitrogen has been identified as a limiting factor for marine vegetation growth (Zhao et al., 2021). In pristine coral habitats, nitrogen is found in very low concentrations and typically comes from sources such as ocean upwelling, nitrogen fixing organisms, and atmospheric deposition (Lapointe, Brian et al., 2021). The limited nitrogen is traditionally taken up by coral zooxanthellae endosymbionts, and it is then used by the microalgae for both their metabolic needs and to sustain an efficient symbiotic relationship (Cunning & Baker, 2012; Lapointe et al., 2019). With increasing coastal human populations, and inefficient management of agricultural and urban runoff, increasing nitrogen enrichment has led to macroalgae blooms that impact coral habitats (De'ath & Fabricius, 2010; Diaz-Pulido et al., 2009; Guo et al., 2019; Lapointe et al., 2021). The use of Chl-a concentrations as an indicator of nitrogen enrichment has been widely accepted to identify macroalgal blooms at early stages. Chl-a is a pigment present in micro- and macroalgae that is used for capturing light for photosynthetic processes. Since nitrogen is commonly a limiting factor, Chl-a levels tend to be low, but when nitrogen enrichment occurs, Chl-a levels subsequently increase, as a result of macroalgal blooms (Bell et al., 2014).

With nitrogen enrichment, and respective elevated Chl-a concentrations due to nitrogen uptake by macroalgae, coral habitats transition into macroalgae-dominated habitats. Across the world, Chl-a and nitrogen concentrations have been examined and compared to macroalgal cover and coral cover. De'ath and Fabricius (2010) described that water quality increased from inshore to offshore areas of the Great Barrier Reef (hereafter referred to as GBR) over 3-fold, whereas chlorophyll was on average 2-fold higher in waters closer to the coasts of Australia. These parameters were compared to macroalgal cover and reef-forming hard coral species. It was found that macroalgal cover decreased approximately 6-fold from nearshore to offshore reefs (De'ath & Fabricius, 2010). On the other hand, hard coral richness was found to double

when moving away from the shoreline, demonstrating that macroalgae out compete corals under these conditions (De'ath & Fabricius, 2010). These patterns have been found to be replicated in other coral regions around the world. For example, in the South China Sea (SCS), Guo et al. (2019) reported that there was a modest relationship between Chl-a concentrations and distance from the mainland. This coincided with a relationship between decreasing dissolved inorganic nitrogen (DIN) concentrations with increasing distance from the Chinese shoreline (Figure 7) (Guo et al., 2019). The process of coral habitats shifting to macroalgal cover occurs via various mechanisms that not only reduce coral health but also affect the ecological dynamics of coral ecosystems. Macroalgal blooms have been linked to the reduced efficiency of strict coral symbiotic relationship with zooxanthellae, extended seasonal algal blooms, and increased populations of coral predating species (Bell et al., 2014; De'ath & Fabricius, 2010; Wang et al., 2019).

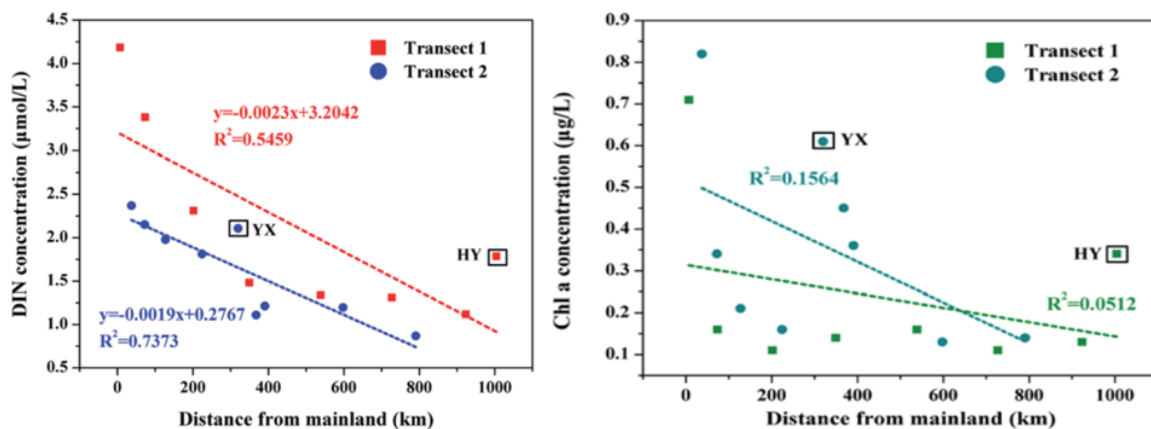


Figure 7. Relationship between DIN and Chl-a concentrations and distance away from the shoreline in the South China Sea. Both parameters are higher when closer to the shoreline, which indicates terrestrial deposition of DIN in the water column, resulting in responsive macroalgae blooms (from Guo et al., 2019).

Generally, the most frequent mechanism of coral cover loss to macroalgae is the competition of macroalgae and coral-symbiont zooxanthellae for resources such as nutrients and sunlight. Firstly, macroalgae blooms promote competition for nutrients such as phosphorus and carbon (in the form of CO₂), which are essential for zooxanthellae growth. Without these

nutrients, macroalgae impact the efficiency of the symbiotic relationship of corals and the microalgae, which is another source of coral bleaching (De'ath & Fabricius, 2010; Lapointe et al., 2019). Since macroalgae grow closer to the surface of the water and take up nutrients more rapidly, these blooms generate shade over benthic communities, including corals assemblages. This results in decreased zooxanthellae photosynthetic rates due to limited light availability (De'ath & Fabricius, 2010). Due to the reduced zooxanthellae metabolic actions, the amounts of by-product carbon (energy) and nutrients provided by the symbiont for coralline metabolic processes are also reduced, leading to coral species experiencing bleaching due to intense starvation (Wooldridge & Done, 2009). These bleaching events create opportunities for other algal species, such as turf algae, which grow on stressed coral tissue, requiring the coral host to produce extra amounts of mucus for cleansing effects. This action requires energy use, which worsens coral health due to the lack of efficient symbiotic relationship with zooxanthellae, leading to coral mortality (Bell et al., 2014). Increased macroalgal cover, and the altered coral-zooxanthellae relationship, induce a negative feedback loop for reduced coral health, where the disrupted symbiotic relationship allows for macroalgal dominance and vice-versa.

Nitrogen enrichment has facilitated macroalgal growth to out compete the coral endosymbiont, which has led to emerging macroalgal dominance of historical coral ecosystems worldwide. The 2006 bleaching event in the GBR uncovered how fleshy macroalgae outcompeted recovering coral colonies (Diaz-Pulido et al., 2009). A large bloom of *Lobophora variegata*, a species of fleshy macroalgae, overgrew coral tissues that were damaged by an unprecedented bleaching event (Diaz-Pulido et al., 2009). In the Caribbean Sea, a seasonal phenomenon has been recently described as the Great Atlantic *Sargassum* Belt (GASB). Wang et al. (2019) defined the GASB as the largest macroalgae bloom in the world, which has been identified to develop since the year 2011. The GASB is characterized to be a seasonal event that mainly occurs during the summer months, with a trend of higher levels of *Sargassum* density in the month of July (Figure 8). This is mainly due to adequate seawater salinity levels and SSTs, but it is mostly driven by seasonal nutrient accumulation (Lapointe et al., 2019; Wang et al., 2019). Though the GASB has not worsened consistently over time, it has been worse in years where nutrient enrichment has peaked in the mouth of the Amazon River and other deltas in

the complex system within the Caribbean Sea (Wang et al., 2019). If not controlled properly, the GASB could become the new norm, and coral assemblages across the Central Atlantic will face an added threat to their already acute susceptibility to anthropogenic impacts.

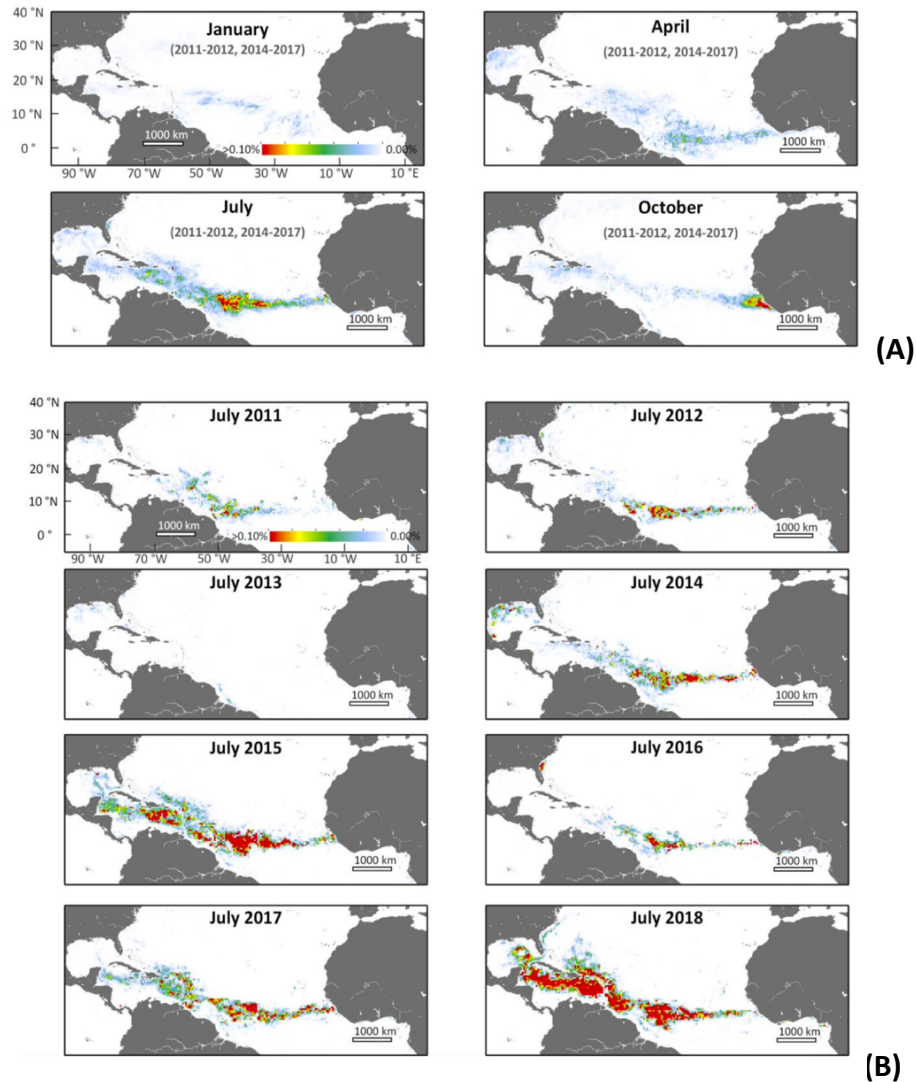


Figure 8. (A) Mean % cover of *Sargassum* density in the months of January, April, July, and October from 2011 to 2017 in the Atlantic Ocean. (B) Monthly mean density of *Sargassum* for July from 2011 to 2018. Note the absence of *Sargassum* bloom in 2013. This shows how the GASB has become a new norm in the summer months in the Caribbean Sea (from Wang et al., 2019).

These macroalgae blooms have been identified in coral ecosystems in the Caribbean region even before the description of the GASB. In the Mexican Caribbean, the increased density of *Sargassum* cover in 2015 was identified as the major cause of coral cover loss in the region (Silva, 2016). In the case of Belize, where a large portion of the Mesoamerican Barrier Reef System (MBRS) is located, escalating macroalgae blooms have been attributed to nutrient enrichment, particularly to increased nitrogen levels. This anomaly has been traced back to anthropogenically-elevated nutrient inputs from major water bodies such as the Belize River, which has resulted in major reduction of LCC in the reef system due to macroalgal overgrowth (Lapointe et al., 2021). In Colombia, a study was conducted by Uribe et al. (2021), where the authors described the need for strict management due to increasing cover of fleshy algae over Colombian coral ecosystems. This study showed that national scale management of nutrient discharge in the Colombian coastal waters was the best approach for alleviating this stress on coral reefs. This is due to nutrient inputs into the seawaters originating from inland terrestrial human activities, a pattern that was identified to experience constant increase since 1998 (Uribe et al., 2021).

In addition to macroalgae blooms, nitrogen enrichment has also been linked with blooms of other algae species such as nano plankton. Nano plankton is usually identified as various species of microscopic algae such as dinoflagellates (Bell, 1992). This type of plankton is a major component of the diet of the larval stage of coral-predating species. For example, in the GBR, increased nano plankton levels coincided with increased populations of *Acanthaster planci*, a species of starfish that feeds on hard corals (Bell, 1992). Moreover, macroalgae blooms also promote increased populations of microbial organisms when the marine vegetation dies and decompose. These organisms require oxygen for metabolic purposes, representing an additional source of competition for corals (Mueller et al., 2014; Webb et al., 2021). These two mechanisms of promotion of coral competing species not only represent a threat to coral cover, but also are advantageous to the outcompeting macroalgae, which benefit from the decaying state of corals to dominate the ecosystem.

4.1.2 Disrupted coral-zooxanthellae symbiotic relationship

As described in previous sections, corals and their endosymbiotic zooxanthellae maintain a loop of nutrient cycling in order to provide each other with the necessary nutrients to prosper. This nutrient cycling is sustained by the previously described oligotrophic conditions, where nitrogen is the limiting factor in zooxanthellae population overgrowth. However, when nitrogen concentrations increase, the conditions for a stable coral and zooxanthellae relationship are altered (Wooldridge, 2020; Zhao et al., 2021). Elevated concentrations of nitrogen enrichment lead to various mechanisms by which the symbiotic relationship is altered, including abandonment of the host by the endosymbiont, contrary expulsion of the microalgae by the coral host, and altered microbiome of coral ecosystems.

One of the most detrimental mechanisms is the expulsion of the endosymbiont from corals as a regulatory instrument (Cunning & Baker, 2012). This scenario has been identified to occur where nitrogen enriched waters promote zooxanthellae population growth. Under elevated zooxanthellae density, the symbionts start to require more carbon for metabolic processes, reducing the host coral's carbon intake (Fuess et al., 2020; Wooldridge & Done, 2009). Increased demand for carbon by the zooxanthellae symbiont has fatal effects on the health of the coral host, which can result in bleaching events and LCC loss. Due to the reduced ability of the coral host to receive carbon, the host experiences limitations in its metabolic processes, leading to coral tissue mortality (Wooldridge & Done, 2009; Fuess et al., 2020). Once tissue mortality takes place, the coral expels the symbiotic cells as a regulatory mechanism with the aim of stopping carbon loss and energetic expenditure in the damaged region. This is because, under stress, it is more energy-costly to repair tissue as the coral is already facing challenging conditions (Cunning & Baker, 2012; Marubini & Davies, 1996). This circumstance presents detrimental conditions for both symbiotic agents. Firstly, zooxanthellae survival is reduced due to the loss of protection given by the coral host from predators. Simultaneously, the coral host's ability to regenerate its damaged tissue is drastically reduced by the absence of endosymbiont's photosynthetic production of essential nutrients, including carbon itself.

In addition to the responsive expulsion of the zooxanthellae symbiont from the coral host detailed above, another mechanism that disrupts this relationship has been described as

apoptosis, which is also triggered by zooxanthellae surpassing the coral host carrying capacity (Lesser, 2021; Wooldridge, 2009). As opposed to the previously described mechanism by which the coral experiences tissue mortality due to the lack of nutrients for metabolic processes, via apoptosis, the coral host induces self-necrosis. This process targets a particular section of coral tissue where the symbiotic relationship is not being performed properly (Wooldridge, 2009). This defensive reaction is generally conducted in the early stages of zooxanthellae overgrowth to prevent further damage. Coral individuals perform apoptosis with the main purpose of not only mitigating tissue damage, but also to sustain a balanced cell environment by choosing to eliminate particular host cells where the symbiotic relationship is not properly functional (Cunning & Baker, 2012; Lesser, 2021).

Nitrogen enrichment has also been found to deteriorate the microbiome of coral reefs, making it a hostile environment for zooxanthellae populations, resulting in the incapability of the symbionts to maintain a stable relationship with their respective coral host. Nutrient enrichment has been shown to promote shifts in the cell-type composition of the microbiome (Becker et al., 2021). This shift has been characterized by the increased density of bacterial cells and other microalgal species in the microenvironment, leading to extra competition for sunlight and nutrients for photosynthetic processes of the zooxanthellae (Shaver et al., 2017). Particularly in the Caribbean, due to its geographical location within the tropics, these microalgae blooms are worsened by the prolonged exposure to more intense sunlight year-round (Lesser, 2021). Moreover, nitrogen enrichment has also been linked to increased bacterial populations. In the Caribbean, a shift to bacterial-dominated microbiomes has been identified, especially from the order *Rickettsia*, which have been identified to potentially act as coral disease-causing organisms as well (Shaver et al., 2017). These shifts in the microbiome do not necessarily reduce zooxanthellae populations but they do reduce the efficiency with which the microalgae conduct metabolic processes, which, in this scenario, leads to the expulsion of the endosymbiont from the coral as the symbiotic relationship is disrupted.

4.1.3 Worsened coral diseases

As the occurrence of coral disease outbreaks has constantly increased in recent decades, the impacts of nitrogen enrichment on these outbreaks have become more evident and detrimental globally (Voss & Richardson, 2006). Various studies have identified the ways in which different forms of nitrogen affect coral diseases, including poorly treated sewage discharge, and agricultural overuse of fertilizers (Voss & Richardson, 2006; Redding et al., 2013). Outbreaks of diseases such as the WSD, BBD, and aspergillosis, have been linked to nitrogen enrichment in the water column, leading to loss of LCC (Kim & Harvell, 2004; Kaczmarzsky et al., 2005, Voss & Richardson, 2006; Baker et al., 2007). The prevalence and the severity of these coral diseases occur via various mechanisms, wherein nitrogen enrichment has been described as one of the contributing factors (Bruno et al., 2003; Kim & Harvell, 2004; Baker et al., 2007). This disease-driving influence of nitrogen occurs through the chemical alteration of the microenvironment, either by increased pathogen virulence, weakened coral tissue, or direct infection of symbiotic zooxanthellae (Bruno et al., 2003).

Globally, poorly treated sewage discharge has been linked to various coral diseases due to deposition of nitrogen in various forms. Particularly, prevalence and severity of diseases such as the BBD and the white syndrome disease have been linked to poorly treated wastewater (Kaczmarzsky, 2005; Redding et al., 2013). This correlation has been described due to wastewater input of $\delta^{15}\text{N}$, a particular nitrogen isotope from human-derived sewage effluents. For example, nitrogen inputs from poorly treated waters were found to have a strong positive correlation with the prevalence of white syndrome disease in Guam, based on the concentrations of $\delta^{15}\text{N}$ (Figure 9 - Redding et al., 2013). Due to the frequency of poorly treated waters in countries along the Caribbean coast, elevated concentrations of $\delta^{15}\text{N}$ have also been identified as an indicator of nitrogen as a major driver of outbreaks of the BBD in this region (Kaczmarzsky, 2005). The frequent linkage between sewage-derived nitrogen and coral diseases continues to demonstrate the importance of proper wastewater treatment strategies to ensure coral health and resilience.

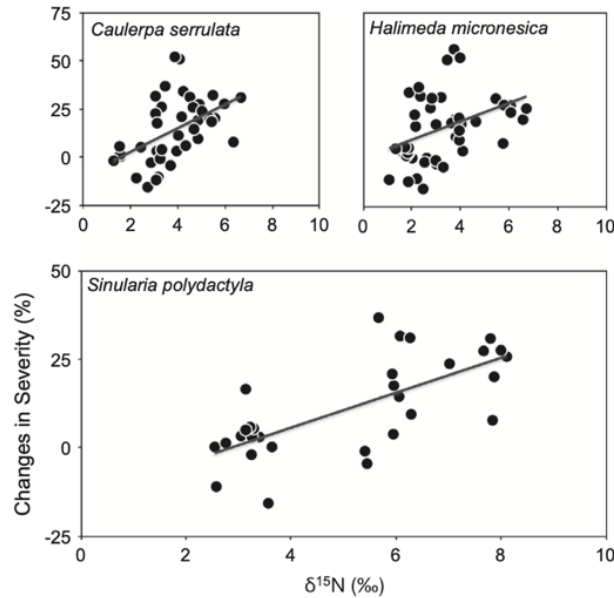


Figure 9. Relationship between nitrogen concentrations and the severity of coral diseases. Note the positive correlation between elevated $\delta^{15}\text{N}$ levels and increased severity of white syndrome disease in three species of corals in Guam (Redding et al., 2013).

In addition to disease outbreaks associated with wastewater discharge, agricultural activities also play a major role in these anthropogenic-induced events. Agricultural activities have been perceived as a major source of nitrogen runoff due to the increased overuse of fertilizers (Voss & Richardson, 2006). Various studies have assessed the impacts of nitrogen enrichment from fertilizers on BBD prevalence on coral ecosystems in the Caribbean (Kuta & Richardson, 1996; Kuta & Richardson, 2002; Voss & Richardson, 2006). Due to the adjacent increased pressure on the land in the form of agriculture, the Florida Keys have become a hotspot for BBD. Here, various BBD outbreaks have been linked to nitrogen enrichment, particularly in the form of nitrite, which results from fertilizer overuse in agricultural lands (Kuta & Richardson, 2002). Nevertheless, although this relationship between runoff of agricultural nitrogen and coral diseases has been more evident in highly developed regions, such as the continental United States, this pattern has also been identified in pristine habitats with relatively small adjacent developed territories. For example, in the coral ecosystems of the British Virgin Islands, it has been found that increased nitrate availability has also facilitated the

spread and severity of BBD outbreaks (Voss & Richardson, 2006). These BBD nitrogen-induced outbreaks were facilitated not only via disturbed host-symbiont relationship, but also by increased populations of coral disease-causing organisms, including cyanobacteria, bacteria from the genus *Beggiato* and *Rickettsia*, among others (Kuta & Richardson, 2002; Voss & Richardson, 2006). Due to the fact that diseases such as BBD have been observed in pristine coral habitats, it is evident how impactful nitrogen enrichment is even at relatively low concentrations.

While diseases such as BBD and the white syndrome disease, among others, are characterized by promoting tissue mortality in corals, other diseases affect coral health in additional manners. In the Caribbean Sea, aspergillosis, an emerging coral disease that has been linked to a fungal infection, targets Caribbean endemic sea fan coral populations (Kim & Harvell, 2004). Aspergillosis is a fungal coral disease caused by the pathogen *Aspergillus sydowii*, which has been identified to proliferate in nitrogen-rich waters, leading to consequential outbreaks due to seasonal elevated nitrogen concentrations in the Caribbean (Kim & Harvell, 2004; Baker et al., 2007). Baker et al. (2007) examined the relationship between aspergillosis prevalence and severity with nitrogen enrichment in the water column. The authors reported that disease prevalence increased with elevated total nitrogen (TN) concentrations, while disease severity was extended by increased dissolved inorganic nitrogen to total phosphorus ratio (DIN:TP) (Figure 10 - Baker et al., 2007). In addition to aggravating coral tissue mortality, aspergillosis in particular has been found to be responsible for reduced coral recruitment and restrained sea fan reproduction (Kim & Harvell, 2004). Diseases such as aspergillosis are of particular concern because it can not only damage existing colonies, but it can also drastically limit coral restoration efforts as it reduces the formation of new colonies by previously mentioned impairment of sea fan coral reproduction.

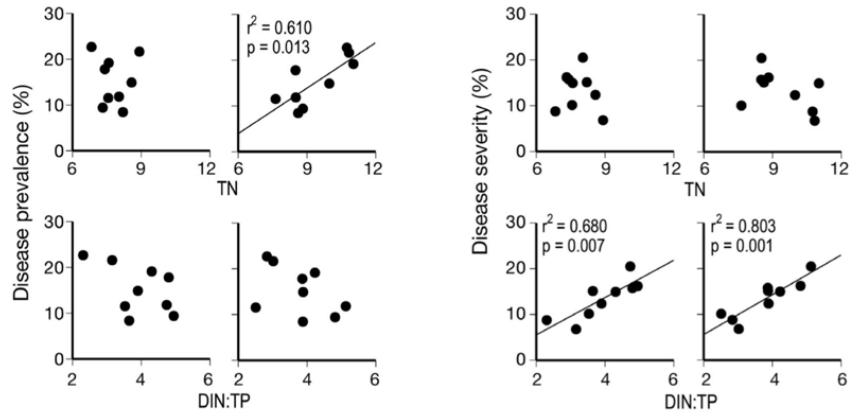


Figure 10. Prevalence and severity of aspergillosis compared to total nitrogen (TN) concentration and dissolve inorganic nitrogen to phosphorus (DIN:P) ratio (Baker et al., 2007).

Coral diseases not only affect coral populations by damaging tissue or limiting the settlement of new colonies but also reduce coral health by aggravating bleaching events. Coral diseases play a substantial role in bleaching events caused by elevated nutrient concentrations in the water column (Cervino et al., 2001; Vega et al., 2014). In a study conducted in 2013, Vega et al. (2014) described that a nutrient induced-bleaching event was highly influenced by the increased occurrence of the dark spot syndrome (DSS). This disease affects various scleractinian coral species, particularly species such as *Siderastrea siderea*, a stony reef-forming coral species endemic to the Caribbean Sea (Cervino et al., 2001; Renegar et al., 2008; Vega et al., 2014). The mechanisms by which this disease affects corals are not completely clear yet. However, many hypotheses state that this occurs via coral pathogens, and others suggest direct infection of the symbiotic zooxanthellae (Cervino et al., 2001; Renegar et al., 2008). Nonetheless, increased occurrence of DSS has repeatedly been linked to nutrient enrichment, particularly to elevated nitrogen levels in coral habitats (Cervino et al., 2001; Renegar et al., 2008; Vega et al., 2014). The case of the DSS in the Caribbean gives a clear example of how nitrogen enrichment promotes coral diseases that are not fully understood yet. This highlights the importance of enhancing coral resilience when facing adversities that humans might not be aware of thus far.

4.2. Indirect impacts of nitrogen enrichment on corals

The mechanisms by which nitrogen enrichment affects coral ecosystems described above have further implications that act as additional indirect impacts on worsened coral health. Namely the shifts to macroalgal cover, disrupted coral-zooxanthellae relationships, and worsened coral diseases also promote other negative impacts on coral health. By worsening coral health, as well as the overall conditions that coral organisms have to face, these direct impacts interact and highly influence the occurrence of indirect impacts, which include the creation of hypoxic zones and altered coral calcification processes. The occurrence of these indirect effects is exacerbated by the incidence of the direct impacts described in the previous section. This situation feeds a loop of detrimental conditions in coral habitats that, if not identified and treated in a timely manner, can represent a long-lasting hostile environment for coral colonies. When facing these adverse environmental conditions, LCC can potentially be reduced to an irreversible point, where coral colonies might not be able to recover.

4.2.1 Creation of hypoxic conditions

Due to the warmer nature of their waters, tropical marine ecosystems tend to maintain DO levels closer to the lower ends of normoxic thresholds (Lapointe & Clark, 1992). Although some studies had previously suggested hypoxia as a potential emerging stressors to tropical coral habitats (Lapointe & Clark, 1992; Lapointe & Matzie, 1996), it was not until 2010 that a study properly assessed the impacts of a hypoxic event on a Caribbean reef (Altieri et al., 2017). Since then, various studies have been able to further describe the development of hypoxic zones in the region, including climate change and altered water stoichiometry due to excess nutrient inputs (van Tussenbroek et al, 2017; Nelson & Altieri, 2019; Johnson et al., 2021). Nitrogen enrichment has played a crucial role in the development of temporary and permanent hypoxic conditions in tropical waters (Nelson & Altieri, 2019; Johnson et al., 2021). Some of these effects are induced by the previously describe direct impacts, which result in increased populations of competing species for corals, the creation of dead zones, and damaged coral microenvironment.

Rapid depletion of oxygen availability, which can be exacerbated by nitrogen enrichment, has resulted in the creation of dead zones promoted by hypoxic conditions during extended periods of time (Johnson et al., 2021). Lapointe and Clark (1992) investigated the relationship between nitrogen enrichment, in the form of ammonium and nitrate, as a result of watershed discharge and oxygen levels in the Florida Keys. The authors noted a negative correlation between nitrate concentrations and distance from the shoreline, as well as a contrasting positive relationship between oxygen levels and distance from the coastline. Moreover, the results also revealed a negative relationship between DO and ammonium concentrations (Figure 11; Lapointe & Clark, 1992). Additionally, various studies have examined how rain events can facilitate these trends of high nitrogen levels and low oxygen concentrations, which is promoted by increased runoff and discharge of terrestrial nitrogen into coastal waters (Lapointe & Matzie, 1996; Lapointe et al., 2019). Nitrogen enrichment is predicted to increasingly provoke the incidence and formation of hypoxic and dead zones in the Caribbean, which can be attributed to recent rapidly growing human population in coastal areas of the region and the rainy tropical characteristics of its land ecosystems. Elevated nitrogen concentrations indirectly promote hypoxic events via various mechanisms such as those described in previous sections, including macroalgae blooms, disturbed coral microenvironments, and by promoting disease outbreaks in coral ecosystems (Nelson & Altieri, 2019; Johnson et al., 2021).

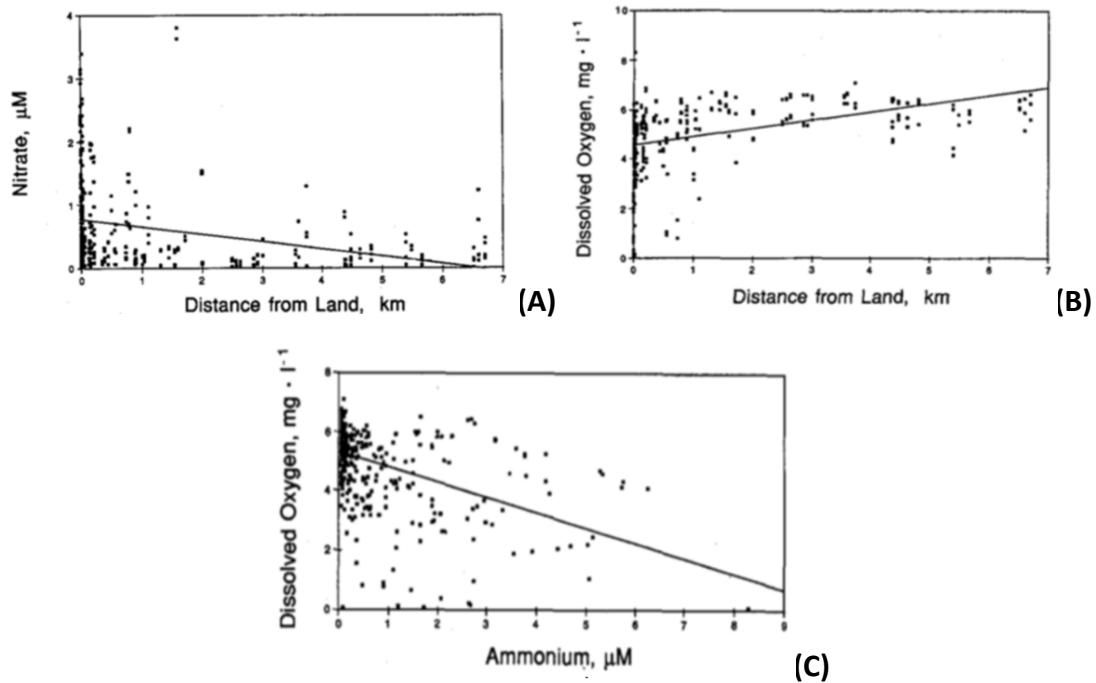


Figure 11. Relationships of (A) nitrate and (B) DO in function of distance to the shoreline, as well as (C) the negative correlation between DO and ammonium concentrations (Lapointe & Clark, 1992).

Different algal blooms induced by nitrogen enrichment promote the formation of local hypoxic conditions. This occurs when (1) macroalgae decompose and subsequently promote microbial populations that compete with coral for oxygen, and (2) when other forms of algae serve as food source for species that also compete with corals for oxygen. Firstly, even when life cycles of macroalgae come to an end, their impacts on oxygen availability continue even after this cycle (Nelson & Altieri, 2019). When macroalgae die, the respective remaining organic matter sinks to the bottom of the habitat, which leads to enhanced microbial populations due to the increased availability of resources. These microbial populations use the oxygen available to conduct decomposition of the dead organisms, which further reduces oxygen availability for already damaged coral organisms (Diaz & Rosenberg, 2008). Secondly, nitrogen enrichment has also been linked to blooms of other plankton species, such as blooms of nanoplankton populations. Nanoplankton has been identified as the major component of the diet of larval stages of other aerobic invertebrates in coral habitats (Bell, 1992). This leads to the addition of

increased populations of competing species, including other cnidarians and echinoderm communities among others. Increased populations of coral competitors for oxygen put coral organisms at risk as hypoxic conditions are simultaneously promoted at macro- and micro-levels.

As aerobic organisms, corals depend on oxygen availability to conduct and meet respiration needs. Though, as explained above, corals rely heavily on oxygen availability in their surrounding environment, corals also need proper transfer of oxygen within their microbiome. Oxygen largely becomes available thanks to the symbiotic relationship with zooxanthellae, which provides oxygen to the host as a byproduct of photosynthetic processes (Johnson et al., 2021). This crucial host-symbiont interaction has been described to occur mainly during the daytime, when endosymbionts usually provide excess oxygen to the coral host. Corals use enough oxygen to conduct respiration, and then release the oxygen surplus to the surrounding environment (Nelson & Altieri, 2019). However, during the nighttime, it has been found that it is normal for corals to experience mild hypoxic conditions due to the absence of light for zooxanthellae photosynthetic processes (Al-Horani et al., 2007). The threat of nitrogen enrichment to DO levels becomes more evident during the daytime, where oxygen is produced by zooxanthellae. As discussed in previous sections, this symbiotic relationship has been degraded on many occasions due to elevated nitrogen concentrations. This disruption limits nutrient cycling between both organisms extending normal nocturnal hypoxic conditions into the daytime (Nelson & Altieri, 2019). These nitrogen enrichment threats to the crucial symbiotic relationship lead to the creation of hypoxic microenvironments between the host and the endosymbiont, which result in the inability of corals to properly conduct respiration processes.

In addition to the alteration of the symbiotic relationship, hypoxic microenvironments are also promoted by shifts to macroalgal cover, indirectly impacting the diffusive boundary layer (DBL). Various studies have described the DBL as a fine layer that surrounds coral colonies where diffusion is the main transfer mechanism of gasses such as DO (Shashar et al., 1993). The layer has been characterized to be formed by just a few millimeters of stationary water, and its thickness has been reported to vary based on factors such as water temperature changes and water flow (Patterson, 1992; Kühl et al., 1995). In the coral respiration processes described

previously, the DBL acts as a regulating interface for gas exchanges with the surrounding environment, therefore, the thicker the DBL, the harder it is for oxygen exchange to occur efficiently (Dennison & Barnes, 1988). When nitrogen-induced macroalgae blooms cover coral habitats, the DBL experiences warmer water temperatures and reduced water flow, increasing the thickness of the layer (Shashar et al., 1993). This thickening of the DBL consequently leads to reduced flow of DO into the coral microenvironment, worsening the already challenging hypoxic conditions during nighttime (Brown & Carpenter, 2013; Jorissen et al., 2016). Moreover, due to the coupling of this mechanism with poor photosynthetic performance of zooxanthellae, hypoxic microenvironments are also extended and worsened during the daytime since, as mentioned previously, this is when most of the oxygen production from zooxanthellae takes place. (Brown & Carpenter, 2013; Jorissen et al., 2016).

4.2.2 Altered calcification processes

Calcification processes have been disrupted and reduced due to nutrient enrichment events, most particularly by elevated nitrogen concentrations (Edinger et al., 2000; Webb et al., 2021). Increased nitrogen in coral habitats has been recognized to affect calcification processes in different ways. Some of these mechanisms include alteration of the stoichiometry of the water column, disturbed coral relationship with their zooxanthellae endosymbionts, shifts to macroalgal cover, pH variability, and increased populations of coral competing organisms (Caroselli et al., 2011; Dunn et al., 2012; Shantz & Burkepile, 2014).

Alteration of the seawater stoichiometry is one of the mechanisms that has been described to have a major detrimental impact on coral calcification processes. The first mechanisms by which nitrogen enrichment affects coral calcification is the lack of carbon for the formation of aragonite. However, this has been described to be context-dependent on the type of nitrogen enrichment: ammonium or nitrate (Zhao et al., 2021). In environments where elevated nitrogen concentrations occur in the form of ammonium, short-term ammonium enrichment has even been found to promote coral growth as the zooxanthellae can grow without exceeding coral carrying capacity. However, with long-term ammonium enrichment, carbon availability has been identified to be reduced due to increased zooxanthellae

populations outcompeting the host (Cunning & Baker, 2012). Here, as described in previous sections, photosynthetic carbon byproduct from zooxanthellae is not transferred to the host for calcification processes. Instead, it gets used by the endosymbiont for its own metabolic needs (Wooldridge & Done, 2009). On the other hand, when nitrogen enrichment occurs in the form of nitrate, the transfer of photosynthetic byproduct carbon is reduced because the reduction of nitrate to ammonium requires extra energy use from the endosymbiont (Shantz & Burkepile, 2014). Here, calcification rates are reduced via lowered energy transfer rather than direct competition for the nutrient between the host and the *Symbiodinium* (Zhao et al., 2021).

In addition to reduced carbon availability, nitrogen enrichment has also been detected to reduce the quality of calcium-carbonate skeletogenesis. Because carbon transfer from the endosymbiont to the host is reduced in nitrogen enrichment events, corals have been found to make a shift from using carbonate ions to use phosphate (PO_4^{3-}) ions, which have the ability to bind with Ca^{+2} as a replacement of carbon, a process known as alternative calcification (Montagna et al., 2006). In this process, phosphate binds with calcium to form the crystal structure and produce the coral skeleton (Simkiss, 1964). Nevertheless, the incorporation of phosphate and calcium (CaHPO_4) for calcification has been found to result in a weaker and more porous coral skeletal structure (Figure 12 - Dunn et al., 2012). This happens because the three-dimensional structure of phosphate differs from that of carbonate, affecting the quality of coral skeleton (Dunn et al., 2012). Although the adaptation of corals to use phosphorus may seem advantageous, the characteristics of this alternative skeletogenesis are not necessarily favorable when facing other environmental adversities, which is due to the increased porosity and instability of the skeleton.

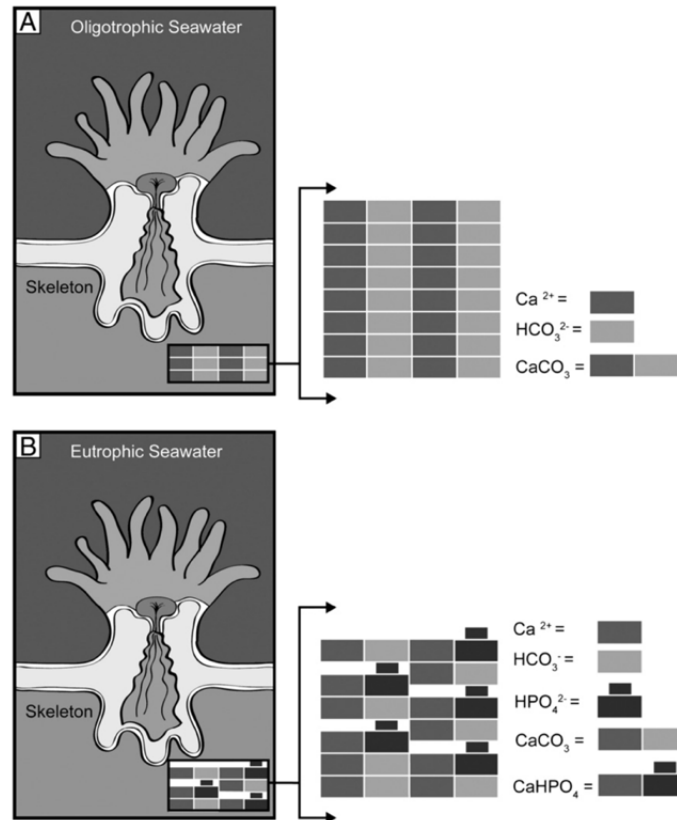


Figure 12. Comparison of the structure of a (A) normal calcium-carbonate (CaCO_3) formed coral skeleton under oligotrophic waters, and a (B) coral skeleton formed via calcium-phosphate (CaHPO_4) bonds under eutrophic waters. Note the increased porosity of the skeleton when calcium binds with phosphate compared to calcium-carbonate bonds (Dunn et al., 2012).

Nitrogen-induced lowered calcification rates and reduced quality of coral skeleton represents a threat to corals as nitrogen enrichment also indirectly alters the pH of the water column (Webb et al., 2021). As discussed in previous sections, nitrogen enrichment has been linked to shifts from historical coral habitats to macroalgal cover and turf algal cover in addition to cyanobacterial mats (Hughes et al., 2003). This shift has resulted in increased concentrations of dissolved organic carbon (DOC), which occurs via decaying turf algae and other macroalgae alongside DOC production by cyanobacteria (Brocke et al., 2015; Mueller et al., 2014). These elevated DOC concentrations enhance heterotrophic activities, which have negative effects on coral habitats by reducing local pH levels due to aerobic use of DO_2 as energy source, and consequent production of carbon dioxide (Webb et al., 2021). Acidic pH levels have not only

been associated with reduced calcification rates, but also with increased dissolution rates (Silbiger et al., 2018; Webb et al., 2021). During dissolution events, the coral skeleton disintegrates, providing exposed bare coral surface for turf algae colonization over damaged and dead tissue, which stimulates a detrimental loop of hindered coral calcification and promoted algal cover.

Even though elevated concentrations of DOC have resulted mostly in increased populations of microorganisms, the populations of coral-excavating sponges have also increased due to higher DOC levels during nitrogen enrichment events (Mueller et al., 2014). Coral-excavating sponges are bioeroding organisms within the family of boring sponges, which are characterized by having ability of drilling holes in calcium-carbonate skeletons that are then used as settlements (Mueller et al., 2014). In nitrogen enriched waters, populations of these organisms increase due to two main conditions: (1) elevated concentrations of DOC as energy source, and (2) previously described increased coral skeleton porosity (Caroselli et al., 2011; Mueller et al., 2014). Boring sponges are known for relying on organic carbon for their growth and other metabolic needs, but it was not until recently that it was found that DOC can constitute over 90% of their diet (Mueller et al., 2014). This has become an emerging challenge for coral calcification in nitrogen polluted habitats, where turf algae, macroalgae, and cyanobacterial blooms result in increased levels of DOC. Secondly, and as described in previous sections, given the increased coral skeleton porosity due to reduced carbon availability, coral-excavating sponges find more opportunities to settle between coral tissue (Caroselli et al., 2011; Shantz & Burkepile, 2014). The elevated presence of coral-excavating sponges not only limits the ability of corals to repair damaged tissue, but it also reduces the opportunity for corals to recruit symbiotic zooxanthellae after nitrogen enrichment episodes, given the reduced availability of space for the microalgae (Caroselli et al., 2011; Shantz & Burkepile, 2014).

4.3. Nitrogen enrichment coupled with other anthropogenic stressors

Although nitrogen enrichment profoundly acts as an adverse stressor to coral health on its own, when coupled with other environmental stressors, not only are these negative impacts exacerbated, but also other unfavorable conditions arise as added challenges for corals.

Anthropogenically-induced stressors on marine habitats such as overfishing, climate change, and OA, continue to add obstacles to coral resilience. Despite the global awareness of the effects of each of these stressors on coral ecosystems (Baker, David M. et al., 2018; Burkepile & Hay, 2009; Serrano et al., 2017), examining the coupling of these effects with those of nitrogen enrichment is important to understand the connectiveness of human activities and deteriorated coral habitats. By identifying how these stressors interact with each other, preventive management strategies can target human practices that can improve coral resiliency.

4.3.1 Nitrogen enrichment and overfishing

Overfishing is one of the major anthropogenic stressors on marine ecosystems because this promotes the extraction of fish species at a faster rate than they can reproduce. As fishing activities have been regulated and particular fishing standards have been placed such as fish size and quantity that can be collected depending on species, overfishing has become a highly selective human activity by which fish communities and their population characteristics are altered (Jackson et al., 2001). As a result of over- and selective fishing, characteristics of fish populations such as average fish size, sex ratios, and fertility rates have been altered (Shantz et al., 2020). Moreover, overfishing not only negatively impacts fish communities, but also takes away their respective ecological role in the ecosystem they inhabit (Burkepile & Hay, 2009; Hughes et al., 2003). When coupled with nitrogen enrichment, overfishing pressure aggravates many of the previously described threats to coral health including shifts to macroalgal cover, reef structure by altered coral predation, reduced coral resilience, and worsened impacts of hypoxic conditions.

Overfishing has been identified to facilitate the shift from LCC to macroalgal cover during nitrogen enrichment episodes. Selective fishing is the main cause of the reduction of herbivorous fish in coastal ecosystems, particularly of species such as parrotfish and surgeon fish (Shantz et al., 2020). In the case of parrotfish species, which are known to be the largest herbivorous species in tropical coral assemblages, their populations have been recognized as indicators of grazing processes in these ecosystems. Therefore, when parrotfish populations are

reduced, macroalgal cover tends to grow more rapidly (Bellwood et al., 2003). Reduced of herbivorous fish in a Caribbean reef has been identified to worsen shift to macroalgal cover when the habitat also experienced nutrient enrichment (Burkepile & Hay, 2009). Additionally, because overfishing impacts larger herbivorous fishes due to the size standards for fishing activities, the reduction of average size of these populations also impairs grazing rates, resulting in macroalgae growth overcoming grazing pressure from remaining herbivorous fish populations (Hughes et al., 2003; Shantz et al., 2020). Moreover, as macroalgal cover promotes hypoxic conditions, this reduced oxygen availability also limits fish populations, which need oxygen to survive. The combination of overfishing and hypoxic conditions creates another positive loop of adverse conditions for herbivorous fishes, taking away their ecological role to help alleviate the conditions that corals face under nitrogen enrichment events.

Additional mechanisms by which overfishing affects coral health is the alteration of reef structure by modified coral predatory dynamics. Firstly, although the diet of parrotfish is mainly based on algae, larger parrotfish species can occasionally feed on exposed coral tissue (Miller and Hay, 1998). Though described to occur very seldomly, this corallivory action tends to be beneficial to reef diversity as parrotfish have been found to target stony corals, resulting in more available space and resources for branching corals (Miller & Hay, 1998; Bonaldo et al., 2011). However, when facing bleaching events induced by nitrogen enrichment, stony corals can outcompete branching corals in recovery processes, which, in habitats where parrotfish are overharvested, can lead to reduced coral diversity (Shantz et al., 2020). Moreover, nitrogen enrichment paired with overfishing of other fish species has also resulted in the increased populations of strict coral predators. As previously mentioned, in the GBR, increased abundance of coral predating *A. planci* had been heavily linked to nitrogen enrichment (Bell, 1992). However, Jackson et al. (2001) added that overharvesting of fish species that prey on *A. planci* also played a crucial role in outbreaks of the populations of this species, resulting in reduced coral cover. These mechanisms show the implication of nitrogen enrichment paired with overfishing on top-down coral reef dynamics.

Though parrotfish corallivory may not be immediately recognized as a positive process, in addition to enhancing coral diversity, this predatory action has also been shown to increase

coral resilience when recovering from events of disturbance. Since parrotfish predation on coral colonies occurs at low but constant rates, coral calcification processes are steadily stimulated, allowing corals to adapt and recover damaged tissue rapidly when facing other adversities such as those of nitrogen enrichment (Shantz et al., 2020). However, in habitats where overharvesting of parrotfish occurs, corals recovery rates are lowered due to reduced efficiency of their calcification processes (Bellwood et al., 2003). Additionally, driven by selective overfishing of larger specimens of herbivorous fish, the reduced average size of these populations has been shown to have a higher impact on reduced coral resilience than fish biomass itself. This means that the absence of larger parrotfish has a higher impact on poor coral calcification than the amount of parrotfish in the habitat (Houk et al., 2014). The absence of constant stimulation of coral calcification has resulted in inefficient coral recovery when facing periodic or seasonal stressors such as nitrogen enrichment, which consequently leads to shifts to macroalgal cover at a faster pace (Bellwood et al., 2003; Burkepile & Hay, 2009; Shantz et al., 2020).

In addition to reduced coral resilience, overfishing also aggravates the impacts of nitrogen-induced hypoxic conditions. Many fish species, especially small species such as those in the damselfish family, are overharvested for aquarium decoration and exhibition purposes (Wabnitz, 2003). When these populations are extracted from their habitats, their role in the respective mutualistic relationship with coral colonies is inhibited. This relationship is based on the coral providing shelter for the fish at night when predation from carnivorous fish is highest. In return, fin movements of the sheltering fishes increase oxygen circulation into the coral's DBL when nocturnal hypoxia occurs (Goldshmid et al., 2004). As described in previous sections, during nitrogen enrichment events, oxygen availability becomes restricted for corals by alterations of the DBL microenvironment (Shashar et al., 1993). During periods of nitrogen enrichment, overfishing of damselfish species such as *Chromis viridis* and *Dascyllus aruanus* reduces oxygen flow through the DBL of the coral host, further limiting oxygen availability for coral respiration purposes (Lieberman et al., 1995; Garcia-Herrera et al., 2017).

4.3.2 Nitrogen enrichment and increasing temperatures

In the current changing climate, anthropogenically-induced global warming has oftentimes been described as one of the major stressors to coral health. Though it is widely recognized that the water column is constantly changing, as seasonality brings variations in seawater temperatures, global warming has made these temperature fluctuations more drastic in severity and duration (Lesser, 2021). As seawater temperatures have been rising in recent decades, it has been identified that corals have a thermal threshold that induces bleaching, meaning that corals have a range of maximum temperatures that they can withstand before bleaching is induced. However, it has been identified that habitats that simultaneously experience elevated nitrogen concentrations present lower thermal resistance, lowering the chances of corals surviving thermal bleaching episodes (Serrano et al., 2017). Nitrogen-enriched ecosystems have been found to have an average thermal bleaching threshold between 1 and 1.5°C lower when compared to oligotrophic locations, which sometimes can be up to 2 to 2.5°C lower (Wooldridge & Done, 2009). The pairing of nitrogen enrichment and thermal stress reduces coral health and thermal thresholds by the disruption of host-symbiont relationship, and by reduction of coral fertilization and larval performance.

The first mechanism by which raising temperatures and coupled nitrogen enrichment reduce coral health is by degrading their relationship with zooxanthellae. It is known that irregular increases in seawater temperature reduces the efficiency of this relationship, which occurs due to increased respiration rates of the microalgae symbiont (Baker et al., 2018). This elevated metabolic action requires energy, which results in the endosymbiont using its photosynthetic products to supply for the now increased energy demand, impairing the host's ability to receive photosynthetic carbon (Baker et al., 2018; Zhao et al., 2021). As described previously, during nitrogen enrichment events, a similar situation happens when zooxanthellae growth rates are favored by elevated nitrogen availability, also resulting in the symbiont's use of its photosynthetic products for its own metabolic needs (Fuess et al., 2020). When the reduced allocation of nutrients from zooxanthellae to the respective host occurs during thermal bleaching events, if the habitat experiences elevated nitrogen enrichment synchronously, the symbiotic relationship is aggravated even further. During these types of events, where the

symbiotic relationship faces multiple stressors, coral resilience is reduced, which may also facilitate shifts in the habitat to be dominated by macroalgae. Diaz-Pulido et al. (2009) described the occurrence of such combination of stressors in the 2006 thermal bleaching event in the Great Barrier Reef, which uncovered how fleshy macroalgae outcompeted the recovery of coral due to nitrogen enrichment.

The combination of thermal stress and nitrogen enrichment not only affects coral relationships with zooxanthellae, but it also affects coral processes at different stages. For example, although the mechanisms are not fully clear yet, Humanes et al. (2016) describe how the coupling of these stressors reduces coral fertility, which might be due to reduction of sperm mobility by thermal stress, and nitrogen enrichment-induced altered microbial composition that can be detrimental for gamete development. Moreover, other coral processes such as larval settlement and survivorship might be altered by the cumulative pressures from thermal stress and nitrogen enrichment. Firstly, not all coral eggs contain zooxanthellae naturally. For coral species with this characteristic, recruiting the microalgae may be challenging due to reduced mobility by thermal stress and reduced zooxanthellae performance under nitrogen enrichment (Bassim & Sammarco, 2003). On the other hand, for those coral species that inherit maternal zooxanthellae, it can be demanding to sustain large microalgae populations due to nitrogen availability, and consequentially settlement is reduced by impaired mobility due to increased temperatures (Serrano et al., 2017). Nevertheless, if corals at larval stage achieve survivorship and settlement, joint thermal and nitrogen enrichment stress make it difficult to progress into later life stages.

4.3.3 Nitrogen enrichment and ocean acidification

Due to constantly increasing anthropogenic emissions of CO₂, OA has become a threat to corals ecosystems due to its negative impacts on ecosystem processes and composition. This human-induced stressor acts in the form of increased CO₂ concentrations in the water column by atmospheric deposition and oceanic absorption, leading to reduced water pH (DeCarlo et al., 2015). Though the effects of OA paired with nitrogen enrichment on coral health are still largely understudied, there has been some evidence of reduced coral cover in tropical waters where

these events have occurred simultaneously (Shönberg et al., 2017). It has been found that challenges for coral colonies when facing OA conditions are further aggravated if the habitat presents nitrogen enrichment. The main mechanisms by which such a combination of stressors compromises coral health include reduced coral calcification rates, increasing skeletal dissolution, and the promotion of macroalgal cover (DeCarlo et al., 2015, Prouty et al., 2017; Johnson & Carpenter, 2018).

The major impacts of OA on coral health are related to coral structure by promoting skeletal dissolution and by limiting formation of coral skeleton. Initially, coral structure is harmed by increased dissolution rates as a result of reduced pH levels. Under increased water acidity, the coral skeleton has shown to experience chemical erosion, exposing its skeleton, and slowly reducing its CaCO₃ levels (DeCarlo et al., 2015; Prouty et al., 2017). This chemical skeletal dissolution is worsened by nitrogen enrichment-induced promoted microbial activity, which can magnify OA by further elevating CO₂ concentrations as respiration rates increment (Webb et al., 2021). Additionally, it has been described how under OA conditions carbon becomes more available as a result of elevated CO₂ concentrations, representing an additional source of carbon for zooxanthellae metabolic needs. Moreover, during nitrogen enrichment events, zooxanthellae populations can outgrow the coral host's carrying capacity due to increased nitrogen accessibility. When these two resources, nitrogen and carbon, become more available simultaneously, this facilitates the abandonment of the host by the endosymbiont (Shönberg et al., 2017). As described in previous sections, the disruption of coral-zooxanthellae relationship inhibits coral calcification due to the lack of nutrients for this crucial coral metabolic need, which places joint OA and nitrogen enrichment as a magnified detrimental combination of stressors on coral skeletogenesis.

Though OA and nitrogen enrichment impact coral health by directly damaging the coral structure, these joint stressors also have indirect impacts on coral colonies. Firstly, though during nitrogen enrichment events limited carbon tends to be the regulating factor for photosynthetic processes, OA conditions increase CO₂ availability, facilitating photosynthesis and giving rise to extended macroalgal cover (Mueller et al., 2014). This reduced water pH results in a loop of reduced coral health and intensified macroalgal blooms. Additionally, short-

term nitrogen enrichment provides resources for crustose coralline algae (CCA), a family of algae that, contrary to macroalgae, favors coral growth by depositing aragonite in the water column, which is used by corals to build their skeleton (Reyes-Nivia et al., 2014). However, OA has shown to inhibit the growth of CCA because, just like corals, these rely on calcification as their growth mechanism (Shönberg et al, 2017). Therefore, long-term nitrogen enrichment paired with OA, resulting in increased macroalgal cover, represent competition for CCA populations, which translates into decreased CaCO_3 sources for coral calcification (Reyes-Nivia et al., 2014; Shönberg et al, 2017).

As a result of the analysis of the impacts of nitrogen enrichment and other stressors on coral, it is evident that is important to monitor events of eutrophication as well as other stressors such as raising temperatures, overfishing, and OA. Now that the most detrimental impacts of these anthropogenic stressors on corals have been identified along with the interactions between them, it is appropriate to evaluate how these can be monitored efficiently and accurately. For this, it is important to know that, though traditional field techniques are valuable, remote sensing has been improving and facilitating data acquisition and processing while also reducing the demand of time and high-cost equipment.

4.4. Remote sensing as a tool for monitoring coral reefs

Historically, the impacts of nitrogen enrichment and other anthropogenic-induced stressors on coral reefs have been monitored using field techniques and *in situ* observations (Dodge et al., 1982; Miller & Müller, 1999; Hochberg, Eric J., 2010). The most generally used techniques include (1) quadrants covering 1-10m, (2) line transects covering 10-100m, and the most extensive (3) manta-tows, which consists of a diver on a boat that makes stops every 10-15m to conduct assessments for a total of 100+m (Hochberg, 2010). However, there are several limitations with these techniques, the most critical ones being spatial coverage, limited consistency, and high costs in terms of both labor and time commitments (Dodge et al., 1982; Miller & Müller, 1999). In response to these limitations, remote sensing has become an emerging resource for management efforts. This technique not only helps to reduce the

limitations described above, but it can also accelerate data analysis processes, cover larger areas, and expand the range of regions that can be assessed as it facilitates data acquisition in remote habitats where physical accessibility can be limited or challenging (Hochberg, 2010; Mumby et al., 2001). As a relatively new and emerging tool, it is important to understand how remote sensing can be applied to coral habitats in terms of habitat characterization and monitoring of water quality parameters, as well as what some of the considerations are when utilizing these tools.

4.4.1 Habitat characterization

In marine sciences, like in most earth sciences, remote sensing is commonly used for habitat characterization. In the case of coral assemblages, habitat characterization is most often performed in ecosystems of shallow waters by reflectance of the bottom of the sea (Hochberg, E. & Atkinson, 2000). Various studies have found ways to integrate imagery from active and passive sensors, expanding the applicability of remote sensing data for management strategies (Hedley et al., 2016; Mumby et al., 2001). Due to their accessibility and affordability, passive sensors, particularly satellite imagery, have become more dominant in the application of remote sensing for coral habitats.

Remote sensing has been successfully used to differentiate benthic sand, coral, and algae cover as well as the transition areas from one type of cover to the next (Figure 13 - (Mishra et al., 2007)). Sand is usually easier to identify due to its particularly high levels of brightness compared to other cover types, generating high light reflectance. Coral cover is usually identified by the radiation coming from the symbiotic zooxanthellae at a wavelength of approximately 550-600nm. Finally, macroalgae can even be identified down to algal type (chlorophytes, phaeophytes, and rhodophytes), depending on their photosynthetic pigment and their respective electromagnetic radiation value (Gokul et al., 2019; Hochberg, 2010; Mishra et al., 2007). This has facilitated the monitoring of coral cover and its changes over time by the application of tools such as time series. This remote sensing application allows for the comparison of habitat characterization at different points in time, allowing to see changes in the composition of the habitats over the desire period of time.

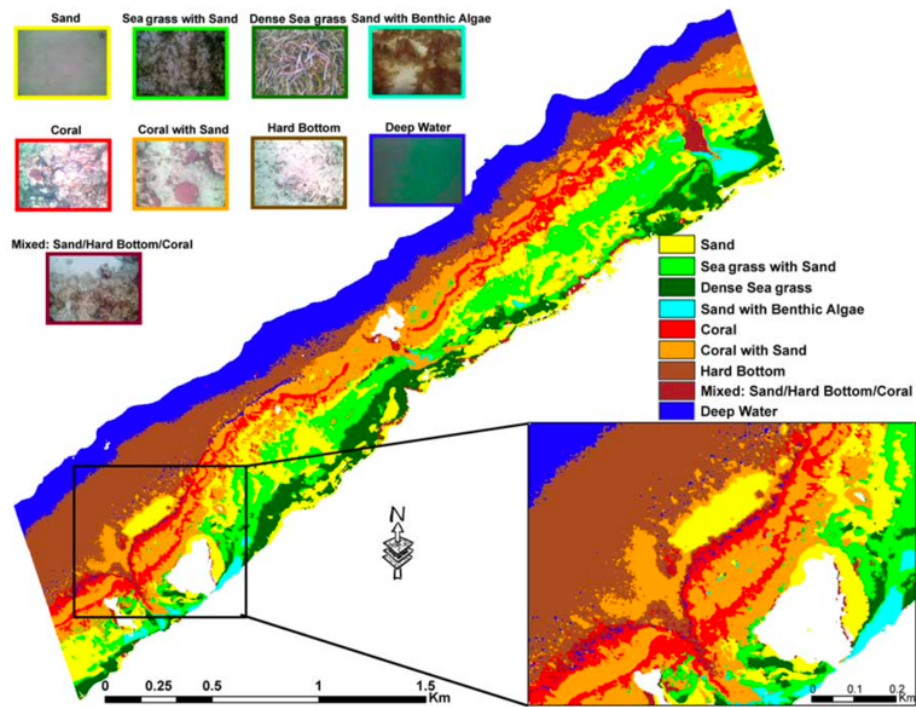


Figure 13. Mapping of a reef habitat using remote sensing. This habitat characterization described 9 types of benthic habitats using unsupervised classification (Mishra et al., 2007).

Coral habitats typically extend for areas of several hundreds of meters or even a few kilometers, and passive remote sensors, such as satellites, are the most commonly used tool to perform habitat characterization at these large scales (Hochberg, 2010). The use of remote sensing imagery from satellites such as IKONOS, Landsat 8, Sentinel-2, and World View-2, with spatial resolution starting from as high as 0.46m, has been identified to be of high accuracy when performing habitat characterization (Mishra et al., 2005; Zeng et al., 2022). Additionally, the use of IKONOS' high spatial resolution of under 1m has delivered precise habitat descriptions allowing for depth characterization, which has traditionally been an obstacle when performing water column correction for mapping coral habitats (Mishra et al., 2005). Furthermore, IKONOS and MODIS imagery have facilitated the identification of cover of invasive and harmful algae blooms over coral habitats, which, when paired with the previous analysis of macroalgal cover over coral habitats, allows for the identification of areas with potential nitrogen enrichment for more strict management (Aandrefouët et al., 2004; Wang et al., 2019).

For example, MODIS and Sentinel-2 imagery identified blooms of *Sargassum* species, an emerging problem in tropical waters referred to in earlier sections (Wang et al., 2019; Wang & Hu, 2021).

In addition to performing coral habitat characterization, remote sensing can be used for classifying land use in adjacent terrestrial areas. This helps to identify what land use changes in terrestrial regions may have an impact on water quality for coral ecosystems (Hedley et al., 2016). Classification of land cover adjacent to coral habitats is a key component of remote sensing as it helps to identify urban development, agricultural and grazing pressure, as well as deforestation events (Lu et al., 2004; Burke et al., 2011). This helps to monitor and identify potential sources of nitrogen that gets discharged in waters with coral habitats, allowing to develop management strategies that target the source of these nutrient enrichment events. Land classification helps to understand patterns in nutrient runoff from different areas within the landscape. For example, increased urban development and agricultural and grazing pressure may help to identify patterns in nutrient enrichment events, increased sediment deposition, and water turbidity (Loughland et al., 2007; Burke et al., 2011). Additionally, loss of natural ecosystems such as wetlands and forest, may also facilitate excess nutrient deposition in waters with coral ecosystems. Such impacts are mainly due to the ability of these ecosystems to filter nutrients and pollutants from entering ocean waters. If the extent of these ecosystems is reduced, these ecosystem services are lost and nutrient enrichment events can become more frequent in seawaters (Gillanders et al., 2008; Burke et al., 2011; Hedley, 2016). Some of the sensors used for these land classification processes include Landsat 5, 7, 8, and Sentinel-2, which provide enough spatial resolution starting as high as 10m (Lu et al., 2004; Gillanders et al., 2008; Hedley, 2016).

4.4.2 Monitoring of water quality parameters

While the most common application of remote sensing targets habitat characterization, other studies have also examined water quality parameters using passive sensors. Via remote sensing, scientists can also compare factors that drive coral health such as Chl-a concentrations, SSTs, and colored dissolved organic matter (CDOM) among others. The combination of these

parameters helps to design and establish water quality guidelines via management strategies that aid coral resilience.

Due to the increased frequency of coral cover loss to macroalgae dominated environments, it has become widely accepted to use water quality parameters to evaluate algal primary productivity such as concentrations of Chl-a (Bell et al., 2014; De'ath & Fabricius, 2010). To measure the level of eutrophication in seawaters, Chl-a has become the most broadly used water quality parameter over coastal coral habitats as a proxy of primary productivity and nitrogen concentrations (De'ath & Fabricius, 2010; Klemas, 2013; Bell et al., 2014; Gokul et al., 2019). This has been true due to two main factors. Firstly, as discussed in previous sections, Chl-a can be used as an indicator of macroalgae blooms, especially during early stages of eutrophication (Bell et al., 2014; Gokul et al., 2019; Klemas, 2013). Secondly, Chl-a concentrations do not always require *in-situ* collection techniques since these can be identified via remote approaches, e.g., satellite imagery, making these measurements cheaper and more accessible (Gokul et al., 2019; Lapointe et al., 2019). This measurement is enabled by the reflection of light from the pigments of photosynthetic organisms, allowing for the identification of regions where species such as macroalgae and phytoplankton blooms prevail or could potentially occur in the near future (Gokul et al., 2019; Lapointe et al., 2019).

In addition to Chl-a, scientists have also been able to use remote sensing to measure habitat temperatures, using SST as a proxy. Due to the known detrimental action of elevated temperatures to coral health, the proxy of SST has allowed for the understanding of thresholds and patterns of temperatures that may induce thermal bleaching (Hedley et al., 2016). This has yielded the development of parameters such as the Degree Heating Weeks (DHW), which allows for the identification of ocean hotspots where SST are 1°C or more above monthly average for a period of 12 weeks (Atwood et al., 1992; Goreau & Hayes, 1994). These temperature anomalies can be monitored via remote sensing, given the ability of sensors to detect thermal radiation. Such ability has allowed for the identification of the potential stages of thermal-induced bleaching such as significant bleaching at DHW values of 4°C for a period of 1-3 weeks, and mass coral bleaching and mortality at values of 8°C after 6 weeks of continued thermal stress (Barnes et al., 2015; Hedley et al., 2016).

Though Chl-a concentrations and SSTs may seem the most dominant indicators of water quality, the quantification of CDOM has become an emerging water quality parameter. CDOM is defined as a substance made up by a mix of molecules that is secreted during decomposition processes of decaying organic matter, such as macroalgae, by microbial activity (D'Sa et al., 2021; Manuel et al., 2021). The inclusion of remotely sensed CDOM as a water quality indicator has become more common due to its ability to absorb UV light, its reflection of visible light fluorescent wavelengths, and the ability of remote sensors to record these spectral behaviors (Chen & Zhu, 2022). While it was initially thought that CDOM's ability to absorb UV light would reduce DNA damage in benthic organisms, it has also been identified that CDOM light absorption capability reduces light penetration into the water column, limiting benthic ecological processes, such as zooxanthellae photosynthetic needs (D'Sa et al., 2021; Manuel et al., 2021). The use of this parameter for coral habitats is of particular relevance, though the presence of organic matter is a natural process, the presence of CDOM has been identified to increase due to sewage discharge and agricultural and urban runoff, serving as an additional indicator of nitrogen enrichment events (Manuel et al., 2021; Mohammadpour & Pirasteh, 2021). Given these characteristics, CDOM has also been used as an indicator of macroalgae blooms and alterations to the carbon cycle in the water column, resulting in reduced coral health and resilience.

Satellite imagery has also shown substantial applicability to find water quality parameters that drive or characterize the types of ecosystem composition described previously. Measuring Chl-a concentration has become widely available through satellites such as Landsat 7, Landsat 8, MODIS, VIIRS (Visible Infrared Imaging Radiometer Suite), and SeaWiFS (Sea-viewing Wide Field-of-view Sensor). The application of these satellites allows for the identification of harmful algae blooms when Chl-a concentrations exceed approximately 0.1 mg/m³ (Guo et al., 2019; Lapointe et al., 2019). For SST trends, the ability of MODIS and POES (Polar Orbiting Environmental Satellite) to track NI thermal radiation has been shown to provide valuable information at spatial resolutions of 250m, 500m, and up to 1.1km (Barnes et al., 2015; Skirving et al., 2006). Moreover, CDOM concentrations have also been quantified by

satellite imagery from sensors such as MODIS, Landsat 7, Landsat 8, and Sentinel-3 (Chen & Zhu, 2022; D'Sa et al., 2021; Manuel et al., 2021; Mohammadpour & Pirasteh, 2021).

Table 1. Different applications of remote sensing and respective passive sensors (satellites), as well as the available spatial resolution for each application offered by the sensors.

APPLICATION OF REMOTE SENSING	SENSORS (Satellites)	AVAILABLE SPATIAL RESOLUTION	CITATIONS
HABITAT CHARACTERIZATION	<ul style="list-style-type: none"> • IKONOS • Landsat 8 • Sentinel-2 • World View-2 • MODIS 	0.46m, 1m, 4m, 10m, 20m, 30m, 60m, 250m, 500m, and 1km.	Aandrefouët et al., 2004; Mishra et al., 2005; Wang et al., 2019; Wang & Hu, 2021; Zeng et al., 2022.
LAND USE CLASSIFICATION	<ul style="list-style-type: none"> • Landsat 5 • Landsat 7 • Landsat 8 • Sentinel-2 	10m, 20m, 30m, 60m, 250m, 300m, 500m, and 1km	Lu et al., 2004; Gillanders et al., 2008; Hedley, 2016.
CHLOROPHYLL-A CONCENTRATIONS (CHL-A)	<ul style="list-style-type: none"> • Landsat 7 • Landsat 8 • MODIS • VIIRS • Sea-WiFS 	28.5m, 30m, 250m, 500m, 750m, and 1km.	Guo et al., 2019; Lapointe et al., 2019.
SEA SURFACE TEMPERATURES (SST)	<ul style="list-style-type: none"> • MODIS • POES 	250m, 500m, 1km, and 1.1km	Barnes et al., 2015; Skirving et al., 2006.
COLORED DISSOLVED ORGANIC MATTER (CDOM) CONCENTRATIONS	<ul style="list-style-type: none"> • MODIS • Landsat 7 • Landsat 8 • Sentinel-3 	10m, 20m, 30m, 60m, 250m, 300m, 500m, and 1km	D'Sa et al., 2021; Manuel et al., 2021; Mohammadpour & Pirasteh, 2021; Chen & Zhu, 2022.

4.4.3 Considerations of remote sensing in coral habitats

Despite the fact that the implementation of remote sensing for coral habitats has evolved and there is an extensive number of resources and applications, there are some considerations that need to be noted when utilizing these methodologies. Firstly, although satellite imagery from sources such as Landsat, Sentinel, and MODIS among others are free to the public, other satellite imagery including IKONOS, which has one of the highest spatial resolutions, may be of relative high cost depending on the extent of the area of interest (Hedley et al., 2016). Additionally, when attempting to obtain data of very high spatial resolution, active sensors might be more useful. However, the acquisition of such specialized equipment might also increase costs, which may be an impediment for organizations or communities with reduced funding (Hochberg, 2010). Additionally, there are some critical water quality parameters that cannot be measured remotely and still need to be collected via field sampling, including DO and pH. Finally, the identification of occurrence of coral diseases via remote sensing is a field that needs more research as there are no current studies regarding this application of remote sensing.

In addition to the described challenges to accessing data, there are some additional challenges when acquiring remote sensing data. Satellite overpasses - meaning when a satellite rotates around the earth and goes over the region of interest - have specific dates and times depending on the particular area of interest, and the satellite that is being used (Hedley et al., 2016; Hochberg, 2010). Some satellites may take twelve, fourteen, sixteen or more days to complete a full rotation around the Earth, which may reduce data availability for short-term studies. For example, a three-month study might only have seven to eight satellite overpasses if the satellite completes a full rotation every twelve days. Additionally, some environmental conditions during satellite overpasses such as cloud cover, water turbidity, and sea surface roughness may alter the quality of the data, reducing the amount of usable information (Hedley et al., 2016). These challenges may be avoided if the stakeholders are able to use active sensors, which can be deployed whenever the conditions align best. Finally, in addition to the remotely sensed data, studies should include some *in-situ* data, which allows to test and validate the accuracy of remote sensing imagery. It is important to consider that this field data

collection should be conducted as close as possible to the time of satellite overpass, or deployment of active sensor respectively, given the rapid variability of the water column (Hochberg, 2010; Zeng et al., 2022).

Finally, when accurate data are obtained, some challenges may appear when processing the information as there are corrections that need to be performed. For example, in the case of cloud cover, cloud masking needs to be applied in order to have usable imagery that excludes pixels with cloud values (Chen & Zhu, 2022). Additionally, atmospheric corrections are needed to reduce the presence of atmospheric gases and aerosols in the imagery, which can distort the quality of the data (Mishra et al., 2007). Furthermore, though satellites use the sun as the source of light, and the sun and the satellite might not always cover the area of interest simultaneously, which results in the light being reflected at a different angle than it is emitted. This produces sun glint, resulting in darker images and making it difficult to record the desired parameters for habitat characterization and water quality accurately (Hochberg, 2010). Despite the fact that these are common obstacles with satellite imagery, there are various studies that have identified methodologies to correct them (Chen & Zhu, 2022; Mishra et al., 2007; Zeng et al., 2022). However, oftentimes these solutions are site-specific, which demands for global applicability of such corrections.

Now that various applications of remote sensing for monitoring coral habitats are evident and described, including ecological processes that occur in these habitats and some water quality parameters that have an impact in the composition of these ecosystems, I will apply these concepts and methodology to a particular region of interest in Colombia. As mentioned previously, the PNN Los Corales del Rosario y San Bernardo is a region of historically extensive coral habitats in the Colombian Caribbean. However, there has also been intensive increased pressure on adjacent land ecosystems due to increased urban development and agricultural activities. This case study will serve as an example of the monitoring and identification of Chl-a concentrations and SST, via remote sensing, in a particular coral region that might be at risk due to nitrogen enrichment.

4.5. Case study

The results of the extraction of Chl-a concentrations and SST for the PNN Los Corales del Rosario y San Bernardo showed a negative correlation between these water quality parameters from 2003 to 2021 (Figure 14). Though there are overall very high mean Chl-a concentrations in the region (highest value 2016 = 1.00 mg/m³; lowest value 2015 = 0.53 mg/m³), these values showed an average decrease during the time frame of the study. Additionally, Chl-a values peaked every four to five years, which might represent some periodic variation due to changes in nitrogen deposition from adjacent land regions. However, the radical increments in 2010 and 2016 were potentially driven by the presence of drastic La Niña events in these years, which could have potentially increased nutrient runoff and discharge from adjacent land regions and watersheds. For the SST values, an overall increase could be identified during the time frame of the study. It is worth to mention that when there were large increases in SST, Chl-a concentrations decreased, and when SST lowered, Chl-a concentrations incremented. This might hint a limitation of the nitrogen-enrichment-induced occurrence of algae blooms due to elevated SST, which is consistent with the existing literature (Hedley et al., 2016; Hochberg, 2010; Lapointe et al., 2019; Wang et al., 2019).

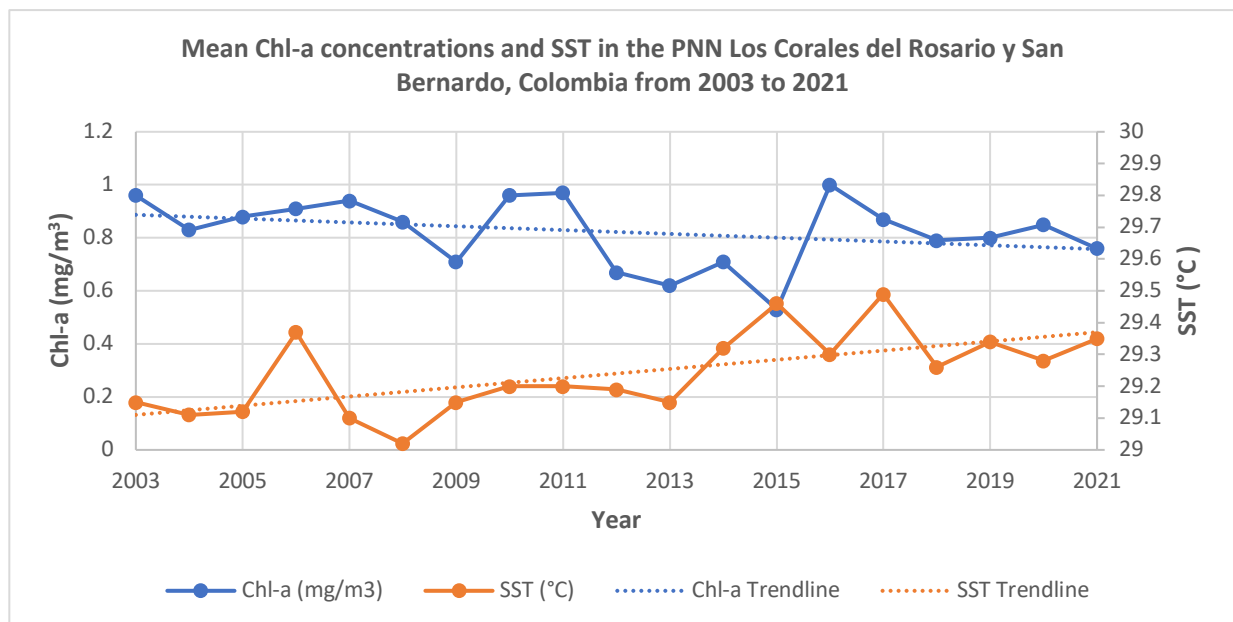


Figure 14. Changes in mean Chl-a concentrations and SST in the PNN Los Corales del Rosario y San Bernardo, Colombia from 2003 to 2021. It is worth to note the negative correlation between the two water quality parameters.

Though Chl-a concentrations in the PNN Los Corales del Rosario y San Bernardo are very high for ideal standards in the Caribbean Sea, these concentrations showed an overall decrease from 2003 to 2021. This might be due to the overlapping increasing SSTs during the same time frame. As described in previous sections, SSTs are detrimental to coral colonies and can promote macroalgae blooms. However, recent research has described that, if risen beyond the threshold of marine vegetation, SSTs can also limit macroalgae blooms (Hughes et al., 2003; Wang et al., 2019). This situation serves as an iteration of the need to apply combined management strategies that not only target one anthropogenic stressor strictly but also aim to progressively reduce various stressors simultaneously. Such need to implement combined management has also been previously identified in the wider Caribbean region including reefs in Belize and in the Florida Keys (Baker et al., 2018; Serrano et al., 2017).

In addition to the relationship between Chl-a concentrations and SST, Chl-a showed additional patterns in spatial distribution within the marine protected area (MPA). The results revealed that Chl-a concentrations tend to be higher in the northern and southern areas of the region (Figure 15). Additionally, Chl-a concentrations were also higher in areas closer to land, which might indicate an influence from land use that resulted in increased nitrogen deposition into the water column.

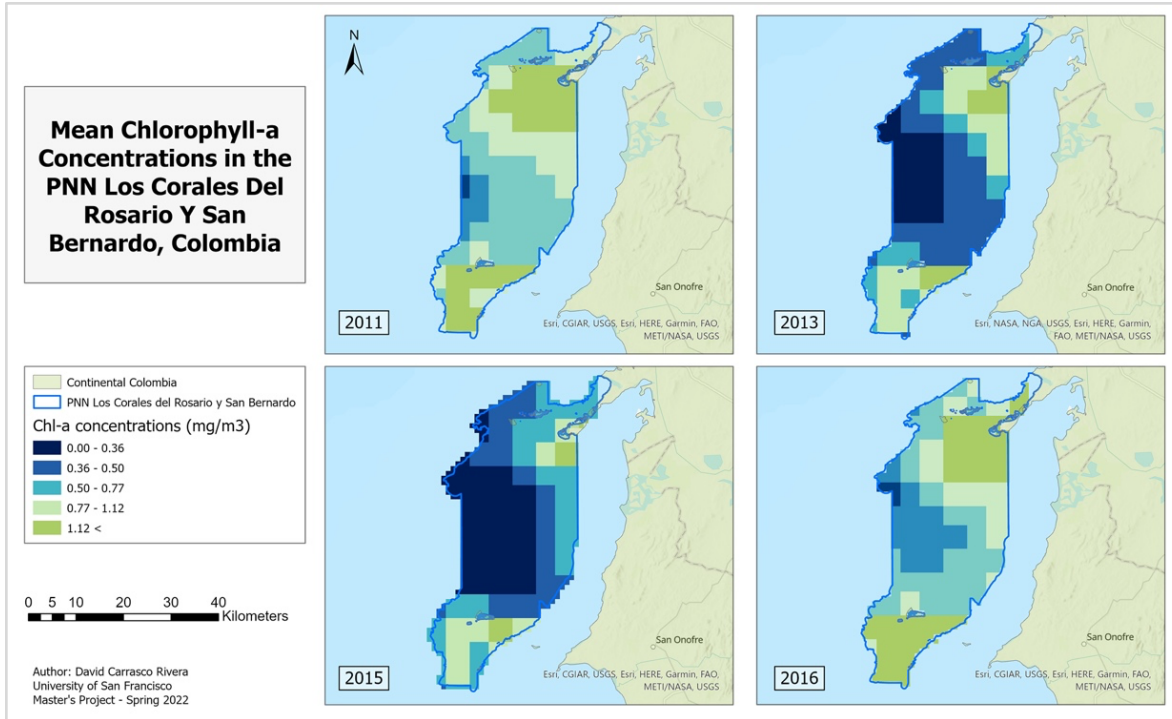


Figure 15. Mean Chl-a concentrations in the PNN Los Corales del Rosario y San Bernardo, Colombia for the years 2011, 2013, 2015, and 2016. These were the years of highest (2011 and 2016) and lowest (2013 and 2015) values of Chl-a concentrations within the time frame of the study. This helps to understand the spatial distribution of Chl-a levels within the MPA. It is worth to mention that concentrations tend to be higher in the northern region of the PNN as well as closer to the mainland.

The case study of the PNN Los Corales del Rosario y San Bernardo serves as an example of the monitoring of Chl-a concentrations via remote sensing. Upon comparing the Chl-a concentrations of the region with standard levels from literature, it is evident that the region is under constant stress due to Chl-a concentration frequently exceeding eutrophication levels of 0.2-0.3mg/m³. This correlation can be explained by the presence and influence of El Canal del Dique (Figure 18). El Canal del Dique is one of the most important waterways for transporting imports and exports of goods in Colombia (Aguilera, 2006; Carvajal, 2015). The presence of this channel not only promotes continuous urban development and agricultural pressure in the region, but it has also heavily modified the landscape (Lonin et al. 2004; Aguilera, 2006). This has resulted in the diversion of a portion of the watershed discharge to flow right above this

MPA. This modification to the landscape and promoted anthropogenic pressure on the land facilitates the understanding of the pattern of higher Chl-a concentrations in northern limits of the region, where a lot of this nitrogen rich discharge is released. The nutrient input from this altered watershed discharge has varied due to the previously described increased urban development and agricultural pressure on the land (Lonin et al. 2004; Aguilera, 2006), allowing for the establishment of a relationship with the overall high levels of Chl-a concentrations in the examined region. This correlation between land pressures and Chl-a concentrations is consistent with the southern region of the MPA, which has been known for heavy presence of agricultural and cattle raising activities. This relationship between Chl-a concentrations and human activities is also consistent with other studies within the Colombian coast (Uribe et al., 2021), in addition to various studies in the wider Caribbean region as well as other coral regions in the world (De'ath & Fabricius, 2010; Hedley et al., 2016; Lapointe et al., 2019; Wooldridge, 2020). Studies of this scope can be used as recommendations to educate decision-making entities and processes, allowing to establish water quality parameters, as well as land use regulations.



Figure 16. El Canal del Dique. The blue line represents the path of the channel from the Magdalena river and into the Cartagena Bay. The green region represents the land area that drains through the channel into the Caribbean Sea (Adapted from Carvajal, 2015).

The case study of the PNN Los Corales del Rosario y San Bernardo also serves as an example of the application of remote sensing tools for environmental management issues. In this situation, MODIS imagery is used to examine two parameters of water quality. Though these results are not validated with *in-situ* data due to the lack of time and resources, which could be implemented in future long-term studies, they do provide a general idea of how to monitor Chl-a concentrations and SST in the region. This sets up an example of how future studies that use remote sensing can apply basic satellite imagery for their region of interest. Additionally, if the scope of future studies allows it, the incorporation of validation and sun glint and atmospheric corrections could be applied for further accuracy. Nevertheless, given the complexity of the understanding, acquisition, processing, and analysis of satellite imagery, it is important to note that it is necessary to promote education in communities where these tools would be helpful, particularly in regions such as the Caribbean countries.

5. DISCUSSION

After an extensive literature analysis of the impacts of nitrogen enrichment on coral habitats, it is evident that shifts to macroalgal cover is the most detrimental mechanism by which coral health is negatively impacted during events of elevated nitrogen concentrations. Although the disruption of symbiotic relationship and increased coral diseases are considered direct impacts of nitrogen enrichment on coral health, these two mechanisms do not necessarily impact coral colonies in as many ways as increasing macroalgal cover does. While the disruption of symbiotic relationship and increased coral diseases affect coral skeletogenesis processes indirectly, these two mechanisms do not necessarily promote the creation of hypoxic conditions: an indirect impact of nitrogen enrichment mostly driven by elevated macroalgae densities. Additionally, the literature review also reveals that increased macroalgal cover induces multiple loops interacting with all the other direct and indirect impacts of nitrogen

enrichment on coral health, while this dynamic is not present for any of the other direct impacts of nitrogen enrichment on coral health (Figure 16).

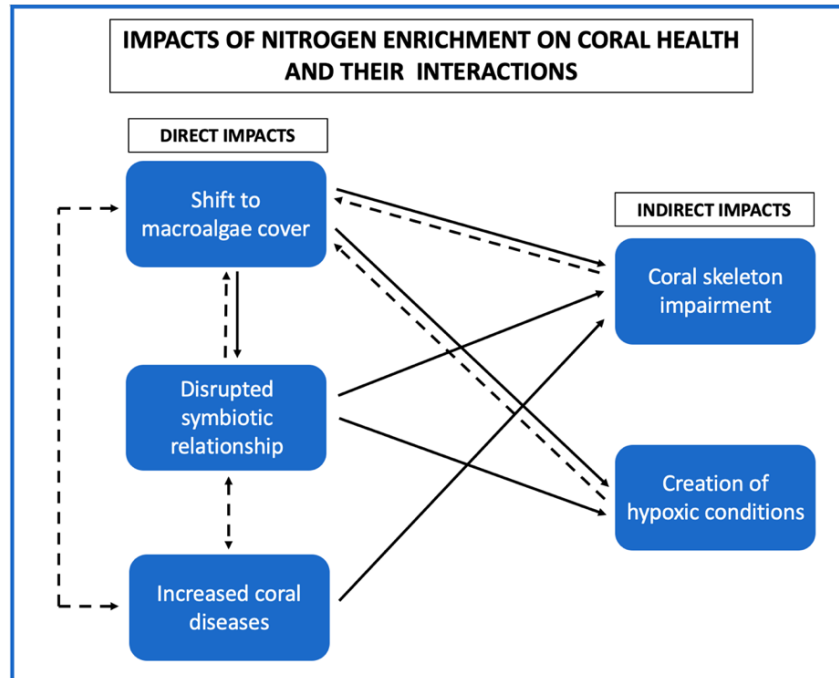


Figure 17. Different direct and indirect impacts of nitrogen enrichment on coral health and their interactions. The solid arrows represent *direct* influence from one impact on the occurrence of the other. On the other hand, the dashed arrows represent *indirect* influence from one impact on the occurrence of to the other. It is worth noting that shifts to macroalgal cover is the only impact that sets up loops of action with all the other direct and indirect impacts on of nitrogen enrichment on coral health.

This situation has been particularly evident in the Caribbean Sea, where coral communities that have become dominated by macroalgal cover have been identified to simultaneously experience other mechanisms by which nitrogen enrichment reduces coral health. Firstly, in the Caribbean Sea, most reef-building corals are part of the *Poritidae* family, which have been detected to lose their endosymbionts more rapidly than other reef-building corals during nitrogen enrichment events (Shantz & Burkepile, 2014). Additionally, these macroalgae dominated ecosystems in the Caribbean have also become hotspots of diseases

such as the BBD, aspergillosis, and the DSS (Kim & Harvell, 2004; Kaczmarek, 2005; Voss & Richardson, 2006; Vega et al., 2014). Moreover, in the Caribbean, nitrogen enrichment has been linked to a shift in microbiomes to be dominated by bacterial organisms, worsening coral diseases and further impairing coral skeletogenesis (Shaver et al., 2017). Finally, due to the already warmer temperatures of the Caribbean waters, already low DO levels facilitate the creation of hypoxic conditions, which have become more frequent as macroalgae blooms have been reported more often in the region (Nelson & Altieri, 2019; Lesser, 2021).

With the information discussed above, it is evident that targeting the prevention of macroalgae blooms is the most efficient way to limit loss of LCC. Monitoring Chl-a concentrations is an efficient way to identify and potentially prevent likely macroalgal blooms and nitrogen enrichment events. Various studies have indicated that Chl-a concentrations between 0.2 to 0.3mg/m³ already indicate eutrophication (Bell et al., 2013; Randazzo et al., 2021). Even though some studies have suggested that some coral assemblages can withstand higher concentrations from 0.45 to 1.75mg/m³ (Guo et al., 2019; Wooldridge, 2020), ecosystems in the Caribbean might be more susceptible to lower concentrations between 0.15 to 0.3mg/m³, which has been evident by situations such as the yearly blooms of the GASB in the region and the emergence of disease hotspots discussed previously (Lapointe et al., 2019; Wang et al., 2019; Randazzo et al., 2021). To ensure that the rigorous standards of Chl-a concentrations are not exceeded in the Caribbean, it is important to regulate human activities in adjacent coastal communities so that nitrogen enrichment can be prevented. This has been proven due to nitrogen enrichment being induced mostly by urban development and poor wastewater treatment, as well as demanding agricultural and grazing activities in land regions adjacent to coral habitats (Lapointe et al., 2019; Randazzo-Eisemann et al., 2021; Voss & Richardson, 2006).

Levels of urban development and agricultural pressure have been rising in countries adjacent to the Caribbean Sea, representing a threat to coral habitats as Chl-a concentrations increase. The impacts of poorly treated wastewaters are of particular concern for the health of Caribbean coral assemblages. Herein, the region is not only experiencing rapid human population growth, especially in the coastal areas, but poorly treated sewage discharge has also

been recognized as the most prominent cause of nutrient enrichment for decades (UNEP, 1998; Hadley et al., 2016). Additionally, given the soil richness of the region, intensive agricultural land use has been recognized as the second major source of nutrient enrichment in the Caribbean Sea (UNEP, 1998; Hadley et al., 2016). The combination of monitoring Chl-a concentrations in coral habitats, alongside the monitoring of human pressures on adjacent coastal land regions, represents a strategy that environmental manager can apply to promote coral resilience.

In addition to macroalgae directly interacting with all the other impacts of nitrogen enrichment alone, this mechanism is also the only one that is worsened when nitrogen enrichment is coupled with any of the other environmental stressors discussed previously. The impacts of nitrogen enrichment were aggravated if the ecosystems experienced events of OA, increased temperatures, or overfishing activities simultaneously. However, after the respective evaluation, shifts to macroalgal cover was proved to be the only mechanism that is affected by nitrogen enrichment coupled with any of the other anthropogenic-driven stressors. On the other hand, neither of the remaining direct or indirect impacts of nitrogen enrichment on coral health were necessarily worsened by all the other stressors (Figure 17).

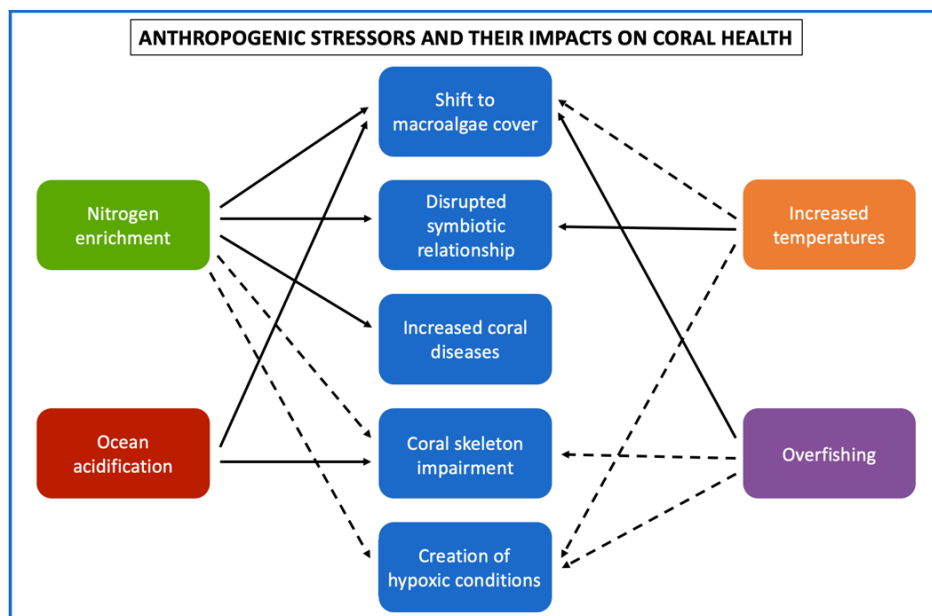


Figure 18. Anthropogenic-driven stressors that represent a major threat to marine ecosystems, and the mechanisms by which these stressors directly or indirectly affect coral

colonies. Solid lines represent a *direct* influence of the stressor on the effect on coral health, whereas dashed lines represent an *indirect* influence. It is worth noting that shift to macroalgal cover is the only mechanism that is directly or indirectly promoted by all the environmental stressors.

Because of the increasing combination of nitrogen enrichment with other anthropogenic-driven stressors in many coral regions, the impacts of shifts to macroalgal cover have become a global concern. Previous research supports the case in the Caribbean Sea, where the most relevant scenario is depicted by the GASB, which has become a new norm in the region for the past decade with yearly blooms of *Sargassum* species (Wang et al., 2019). Additionally, other macroalgae species, such as *L. variegata*, have become highly abundant to the point where many coral ecosystems of the region have become dominated by this brown algae species (Diaz-Pulido et al, 2019). As a result, these shifts to macroalgal cover have reduced LCC in many local ecosystems in the wider Caribbean region including communities in México, Belize, and Colombia among others (Silva, 2016; Lapointe et al., 2021; Uribe et al., 2021). Such situations have been identified to occur in ecosystems that experience nitrogen enrichment coupled with either overfishing pressure, increased temperatures, or OA (Burkepile & Hay, 2009; Serrano et al, 2017; Johnson et al., 2021).

As a response to the impacts of nutrient enrichment and other stressors on corals, local conservation efforts have traditionally focused on identifying the single major anthropogenic stressor on particular local coral reefs to develop management and restoration strategies. However, novel research has demonstrated that this strategy of implementing efforts to tackle the impacts of a singular anthropogenic stressor on coral habitats is not efficient (Asner et al., 2022; DeFilippo et al., 2022). This highlights the importance of developing management strategies that simultaneously target the mitigation of multiple stressors and can maximize coral health and resilience (Asner et al., 2022; DeFilippo et al., 2022). For example, as described previously, when nitrogen enrichment occurs synchronously with thermal bleaching events, overfishing pressure, and/or OA, coral recovery is greatly reduced, resulting in facilitated macroalgal colonization of the ecosystem (Diaz-Pulido et al., 2009; Shantz et al., 2020). The

combination of these stressors reduces the chances of single-stressor management and restoration efforts to find success. Therefore, it is essential to develop restoration and management strategies that guarantee a coordinated series of parameters that enhance coral resilience such as ensuring effective water quality guidelines, regulating coastal development, reducing CO₂ emissions, and strictly delineating marine protected areas with known coral habitats (Asner et al., 2022; DeFilippo et al., 2022).

To develop these coordinate management strategies effectively, it is also necessary to provide accurate and precise scientific information via various methodologies. It is evident that not all communities have the financial resources to conduct extensive field sampling techniques. Therefore, remote sensing is an important tool that not only provides free or low-cost access to data acquisition and processing techniques but also allows for accessibility to remote coral habitats that might be challenging to get to physically. However, it is important to note that remote sensing is only accurate when validated with some field sampling (Hochberg, 2010). Additionally, though remote sensing facilitates the monitoring of water quality parameters such as Chl-a, SST, CDOM, turbidity, and suspended solids, field sampling techniques are still necessary for other water quality parameters such as DO and pH, which cannot be measured via remote sensing yet (Hochberg, 2010; Hedley et al., 2016). Finally, remote sensing is also useful when identifying changes in land use in terrestrial habitats such as agricultural and grazing pressure, urban development, and deforestation events, which are of importance when developing the coordinated management strategies described previously (Lu et al., 2004; Gillanders et al., 2008; Hedley, 2016).

6. RECOMMENDATIONS

One purpose of my research was to provide knowledge about the different direct and indirect impacts of nitrogen enrichment on coral health. My review also aimed to evaluate the application of remote sensing on the monitoring of environmental conditions in coral habitats. The combination of these two approaches allowed me to evaluate applications of remote sensing for monitoring water quality parameters that reduce coral health using proxies such as Chl-a, SST, and CDOM, while also evaluating linkages with terrestrial land use. Insight across

these components identifies a series of recommendations that provide information for policy- and decision-making processes and entities, which can potentially lead to the establishment and development of appropriate and effective management strategies.

In the first place, due to the major implications of shifts to macroalgae blooms over coral habitats, monitoring these events is not only best for identifying where nitrogen enrichment is occurring, but it can also provide insights about how to best prevent loss of LCC. Additionally, if identified at early stages, it can be prevented more easily than having to deal with large biomasses of marine vegetation that can be more difficult and costly to remove. Macroalgae blooms have been shown to aggravate other challenging conditions that impact coral health such as disrupted symbiotic relationship with zooxanthellae, increased prevalence of coral diseases, increased hypoxic conditions, and impaired coral calcification processes. **Therefore, targeting the monitoring of macroalgal blooms is necessary as a preventive management strategy of nitrogen enrichment**, which would alleviate the pressure of the other impacts of nitrogen enrichment on coral health. When monitoring nitrogen enrichment events targeting macroalgae blooms, **evaluating Chl-a concentrations is the best approach for identifying these events at early stages**. The oligotrophic nature of coral environments limits the production of Chl-a in the water column, any increases in this water quality parameter, if identified in a timely manner, can be regulated efficiently. This allows for the implementation of urgent preventive management potentially before macroalgal blooms occur. As a result, this type of management will help to reduce the other direct and indirect impacts of nitrogen enrichment on coral health discussed previously.

To efficiently limit further LCC loss to algal blooms, considering that coral colonies in the Caribbean Sea are particularly more susceptible to increased macroalgal cover than other coral regions in the world, **it is crucial to establish strict water quality parameters that target Chl-a concentrations to remain below 0.3mg/m³ in the wider Caribbean region** (Lapointe et al., 2019; Randazzo et al., 2021). Though this can be a challenging process, gaining support from the public is essential so that policies are more easily implemented as well as properly met. However, this will give coral colonies in the region the opportunity to recover from previous damage and to build resilience when facing other environmental stressors. This can be done

through various environmental management strategies. Initially, by monitoring and regulating land use activities, specifically agricultural and grazing activities, urban development, and deforestation events, as these are the anthropogenic activities that have the most influence in coastal water quality (Lu et al., 2004; Gillanders et al., 2008; Hedley, 2016). Additionally, governments need to make sure that wastewater treatment facilities are properly placed in coastal regions, which will help to alleviate the pressure of pollutants and excess nutrients from entering coral habitats as a result of poorly treated sewage discharge (Baker et al., 2007; Kaczmarek et al., 2005). Finally, by protecting terrestrial natural ecosystems such as wetlands and forest, a lot of these excess nutrients can be filtered naturally before they get deposited into coastal waters (Hedley et al., 2016). This preventive management will allow for the Chl-a parameters to be met properly.

Although water quality is essential for enhancing coral recovery and resilience, to further limit the occurrence of these algae blooms, **it is necessary to implement coordinated management strategies that aim to simultaneously reduce other anthropogenic stressors such as increased temperatures, OA, and overfishing pressure in coral regions** (Asner et al., 2022; DeFilippo et al., 2022). This can be successfully achieved by regulating and reducing emissions of CO₂, which would reduce atmospheric depositions of this greenhouse gas in the water column, alleviating thermal stress as well as events of OA. However, it is necessary to acknowledge that this strategy needs to be applied at a wider and global scale rather than simply at a local scale. Moreover, it is necessary to strictly delineate and reinforce marine protected areas over historical coral habitats, which would translate in the reduction of overfishing pressure over these ecosystems, ensuring the presence of herbivorous fish and their ecological role of controlling marine vegetation (Burkepile & Hay, 2009; Randazzo et al., 2021).

The implementation of remote sensing techniques serves as a rapid tool to monitor where adjustment to water quality parameters need to be urgently enforced. Remote sensing also allows for the monitoring of land use activities, which can facilitate the identification of land regions where better management needs to be implemented (Hedley et al., 2016; Hochberg, 2010). When applying remote sensing techniques for the management of coral habitats, it is important to consider that, to increase accuracy, it is necessary to incorporate

atmospheric and sun glint corrections. Moreover, though remote sensing allows for the monitoring of water quality parameters such as Chl-a, SST, and CDOM, some other critical parameters, such as DO and water pH, still need to be measured with field techniques. Additionally, with the purpose of validating remote sensing data and products, it is necessary to conduct field sampling techniques to collect *in-situ* data for accuracy assessment purposes of Chl-a, SST, and CDOM to provide accurate and precise information for decision- and policy-making processes and entities. **Therefore, it is necessary to combine remote sensing and field techniques to more accurately and effectively monitor and design management strategies.** Finally, though different remote sensing devices provide different resolutions, and resolution needs may vary depending on the scope of the study, implementing medium-to-high resolution is generally desired (e.g., 10, 30, 60m), which increases accuracy of the information to be used for the development of management strategies and targets.

Finally, it is necessary to invest in the education of coastal communities that immediately interact with coral ecosystems. This will not only make them aware of the challenges of nitrogen enrichment and other environmental stressor, but it will also allow them to learn the use, interpretation, and implementation of remote sensing tools. To accomplish this, it is necessary to train and educate local communities via various strategies. Initially, citizen science projects where local fishermen are trained to identify events of eutrophication is crucial, which can be as simple as reporting events of increased macroalgal cover, outbreaks of coral diseases, or even physical changes in the water column such as turbidity or increased sedimentation. Additionally, granting younger generations with access to and encouraging them to take part in training courses where they learn the science behind nitrogen enrichment on corals is necessary. Moreover, it is also fundamental to teach them how to implement different field and remote monitoring techniques. With education particularly, it is important to promote fields that prepare students to learn applied science, programming, and data acquisition and analysis techniques so that remote sensing can be effectively used and applied to the management of their surrounding ecosystems. Finally, by promoting and supporting responsible eco-tourism, where local communities are benefited from the revenues of such activities, will raise awareness in locals and tourists. This will result in adequate interactions

with coral habitats as well as making local communities more interested in the proper management of their ecosystems. These strategies will integrate locals in decision making processes and help them to connect better with their ecosystems.

7. CONCLUSIONS

Nitrogen enrichment has various direct and indirect impacts. Directly, nitrogen enrichment promotes the shift of historical coral habitats to macroalgal dominated ecosystems, the disruption of coral's symbiotic relationship with zooxanthellae, and increased frequency and severity of coral diseases. These direct impacts promote indirect effects including reduced coral calcification rates as well as the creation of hypoxic conditions. Particularly, the shift to macroalgal cover is the most detrimental of these impacts as it promotes and aggravates all the other direct and indirect impacts of nitrogen enrichment on coral colonies. Additionally, when coral habitats experience additional anthropogenic stressors such as overfishing pressure, raising temperatures, and OA, these shifts to macroalgae are further aggravated. As a result, monitoring Chl-a concentrations can help to identify events of nitrogen enrichment at early stages and prevent further damage to coral colonies due to macroalgae blooms.

To monitor these Chl-a concentrations, along with other various water quality parameters, remote sensing represents a helpful tool. Remote sensing not only helps to alleviate some of the costs associated with field techniques, but it can also help to expand the scale of regions that can be monitored, as well as to assess regions that are challenging to access physically. However, it is evident that combining remote sensing techniques with field techniques is encouraged to provide more accurate and precise information for decision- and policy-making processes. Finally, this scientific knowledge and monitoring techniques are only truly beneficial when local communities understand the meaning of the information and can transform it into adequate management strategies. Therefore, promoting environmental education and local participation in decision-making processes is of substantial importance in communities that interact with and rely on coral habitats and their associated ecosystem services.

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