

# **Assessing the potential impact of a mass coral bleaching event on Red Sea fisheries**

Thesis by  
Claire T. Shellem

In Partial Fulfillment of the Requirements  
For the Degree of  
Master of Science

King Abdullah University of Science and Technology  
Thuwal, Kingdom of Saudi Arabia

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EXAMINATION COMMITTEE PAGE

This thesis of Claire T. Shellem is approved by the examination committee.

Committee Chairperson: Prof. Michael Berumen

Committee Members: Prof. Burton Jones, Dr. Darren Coker

## ABSTRACT

Assessing the potential impact of a mass coral bleaching event on Red Sea fish communities, fisheries and ecosystem services

Claire T. Shellem

Worldwide, coral reefs are recognized as highly valuable ecosystems offering numerous environmental and economic services. In Saudi Arabia, the primary ecosystem service derived from coral reefs is the support of reef-based fisheries, accounting for ~75% of total fisheries landing in the kingdom. Saudi Arabian reefs experienced high fishing pressure for decades due to the growing population and associated fishing pressure. Despite the importance of the provisioning service there are limited ecosystem services valuations for this region. In the wake of a 2015 mass bleaching event, we quantified the effect of habitat degradation on the potential fisheries revenue in the central southern Red Sea. We conducted *in situ* reef fish surveys in 2014 and 2015 before the bleaching event and in 2019, nearly four years after the bleaching event. Using species-specific prices collected from local fish markets, we calculated values per hectare from multiple reefs in this region, to assess how the reef-based fishery was impacted by the bleaching event. A loss in live hard and soft coral cover was recorded after the bleaching event with associated shifts in the dominance of commercially important fish species. Notably, prior to bleaching, a larger proportion of the high value carnivorous species (70% carnivores, 25% herbivores) dominated the fish assemblage whereas post-bleaching reefs had a higher dominance of lower-valued herbivorous species (25% carnivores, 50% herbivores). While the total revenue was not significantly different before (7,913 USD/hectare) to after the bleaching event (6,814 USD/hectare), the loss of high value species observed suggests that if reefs continue to degrade there are potential negative flow-on effects impacting fisheries provisioning with time. Overall, an increasing percentage of live hard coral cover was positively correlated with fisheries revenue per reef, further providing evidence for the potential loss of revenue in degraded reef ecosystems in the region.

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## ABBREVIATIONS

CFP—Common Fisheries Policy  
CPP—Coral Point Count  
ENSO—El Niño Southern Oscillation  
ES—Ecosystem Services  
EU—European Union  
KSA—Kingdom of Saudi Arabia  
MEA—Millennium Ecosystem Assessment  
MOA—Ministry of Agriculture (for the Kingdom of Saudi Arabia)  
MPA—Marine Protected Area  
nMDS—Non-Metric Multidimensional Scaling  
NOAA—National Oceanic and Atmospheric Administration  
PCA—Principal Component Analysis  
PERMANOVA—Permutational Multivariate Analysis of Variance  
PERSGA—Regional Organization for the Conservation of the Environment in the  
Red Sea and Gulf of Aden (previously called: Programme for the Environment  
of the Red Sea and Gulf of Aden)  
SIMPER—Similarity Percentage  
UN—United Nations  
UVC— Underwater Visual Census

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## INTRODUCTION

### *1.1. Ecosystem Services*

Ecosystem services (ES) are the many, wide-ranging benefits that humans derive from our natural ecosystems. These services are divided into three broad categories: i) provisioning, which include lumber and fishing industries, ii) regulating and maintenance services which include carbon sequestration, nutrient cycling and coastal protection, and lastly iii) cultural services which includes recreational activities. Most ecosystems provide multiple services, often spanning all three categories. One of the inherent challenges to calculating valuations associated with ecosystem services is that many of these services are not directly marketable. While provisioning services often have a direct market value, most regulating and maintenance services do not (Costanza et al. 1997). It is more difficult to determine a value for the coastal protection that a mangrove forest provides, or the preservation of biodiversity that coral reefs offer than the revenue that can be generated from fishery landings in a region. This is one of many challenges to calculating ES valuations. Additionally, ecosystem services is a relatively young area of study only gaining popularity around the start of the 21<sup>st</sup> century. In 2001, the United Nations (UN) commissioned the Millennium Ecosystem Assessment (MEA) in an attempt to provide context for the repercussions of ecosystem changes to humans and to understand the science behind those changes in order to promote conservation and sustainability for the future. The MEA report was published in 2005 and concluded that in recent history, humans have drastically altered our natural ecosystems and these changes will

persist and worsen, particularly in the face of climate change and an ever-growing population, unless major policy improvements occur. Arguably the greatest result of the MEA, was that it triggered a massive increase of research in the field of ecosystem services (Liquete et al. 2013). Ecosystem services assessments highlight the benefits that naturally functioning ecosystems provide. These assessments are vitally important for their application in policy making decisions (Arkema et al. 2015; Weijerman et al. 2018). When conflicts between stakeholders, government agencies or resource users arise, ecosystem services frameworks can help to highlight all the benefits of an ecosystem, assist with trade-offs and identify the most valuable services. Monetized values of ecosystem services can be used as a persuasive tool to increase awareness and display ecosystem importance and biodiversity to policy makers and resource users (de Groot et al. 2012). These assessments underscore which functions of an ecosystem are the most valuable, indicating potential priorities for protection. However, conducting these assessments is particularly difficult in marine ecosystems where both the services and resource users are abundant. Studying the marine environment is inherently more difficult than terrestrial environments; and for this reason, ecosystem services are far more widely used in terrestrial contexts than marine systems (Townsend et al. 2018).

*Table 1. Table displaying the three types of ecosystem services (Provisioning, Regulating & Maintaining, Cultural), with examples, that occur in the marine environment. Adapted from Lique et al. 2013.*

Provisioning	Regulating & Maintaining	Cultural
Food provision (e.g. fisheries)	Water purification	Symbolic and aesthetic values
	Air quality regulation	
	Coastal protection	
Water storage and provision	Climate regulation	Recreation and tourism
	Weather regulation	
	Ocean nourishment	
Biotic materials and biofuels	Life cycle maintenance	Cognitive effects
	Biological regulation	

Despite the challenges associated with studying the marine environment, marine ecosystems are appreciated for their numerous benefits. Studies of marine ecosystems represent less than 10 % of all ES studies yet the marine environment covers over 70% of the earth and is responsible for 60% of the global ES value annually (20,949 billion USD per year) (Costanza et al. 1997; Lique et al. 2013; Townsend et al. 2018). Provisioning services in marine ecosystems include fisheries, harvesting of coral for lime, timber from mangrove forests and mining. Coastal regions are particularly high in value; mangroves, sea grass beds and fringing coral reefs all play vital roles in coastal ecosystems including coastal protection from storms, water purification and important nutrient cycling processes (Table 1). Cultural services in marine ecosystems range from recreational snorkeling and diving to watching a sunset over the ocean. Among all marine ecosystems, coral reefs are

regarded as the highest in value, garnering 352,915 USD/hectare/year globally, more than twice the value of the next most valuable ecosystem type (Costanza et al. 2014). Coral reefs provide services in all three categories of ecosystem services (provisioning, regulating and cultural), which contribute to a global sum of 30 billion USD annually (Albert et al. 2015; Arkema et al. 2015). The marine and coastal ecosystem services are more valuable than terrestrial ones (Costanza et al. 1997), yet the risks to which they are exposed are numerous. These include global threats (e.g., climate change and ocean acidification) and local threats (e.g., coastal development, pollution and overfishing) which can cause shifts in species distribution and loss of ecosystem function (Arkema et al. 2015; Cheung and Reygondeau 2016). Marine ecosystem services are beginning to be incorporated into policymaking decisions around the world. The Aichi Biodiversity Targets, an initiative from the Convention on Biological Diversity of the United Nations (UN), note the application of ecosystem services in their Target 19: “By 2020, knowledge, the science base, and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied.” (Aichi Biodiversity Targets, n.d.). Belize, after realizing the value of their coral reefs, in 1996 became one of the first countries to require a spatial plan that integrates scientific findings with local knowledge to ensure that their marine ecosystems are managed effectively (Arkema et al. 2014). The application of marine ecosystem services in policy decisions in the eastern Red Sea is extremely limited.

### *1.2. Coral Reefs in the Red Sea*

While the Red Sea is home to expansive coral reefs, seagrass meadows and mangrove forests, all of which are highly valuable ecosystems, there have been very few ecosystem services studies conducted in this region. This knowledge gap was highlighted when a Web of Knowledge search with keywords “Ecosystem Services” and “Red Sea” yielded merely 19 publications, only two of which discussed both ecosystem services and the Red Sea, neither of which discussed the provisioning service. Because different regions worldwide have varying priorities for their ecosystems, management regimes are not easily transferrable between regions (Townsend et al. 2018). For example, worldwide, the most “valuable” benefits of coral reefs are tourism, coastal protection and fisheries; however, for Saudi Arabian coral reefs, that is not necessarily the case. Although international tourism in the Kingdom of Saudi Arabia (KSA) is expected to grow in the next decade (Farag 2019), there is currently very limited international tourism occurring on Saudi Arabian coral reefs, unlike the Great Barrier Reef and the Caribbean Sea regions. Additionally, due to the topography of the Red Sea basin, large storms such as hurricanes, cyclones and tsunamis are highly uncommon in the region. For that reason, coastal protection is less “valuable” in this region than others worldwide. Therefore, the provisioning service of coral reef fisheries can be regarded as currently the most valuable service provided by reefs in Saudi Arabia. Unfortunately, there are numerous threats to this service in the Saudi Arabian Red Sea.

Anthropogenic stressors have increased dramatically in recent decades. These stressors include, at the global level: warming temperatures and ocean acidification, and at the local level: overharvesting and destruction of habitats. Healthy ecosystems are vital to the resilience of natural habitats. With more stressors present, the ability for a habitat to recover is reduced (Costanza and Mageau 1999). A healthy ecosystem has the ability to maintain its structure and function and the ability to recover from external threats (Costanza and Mageau 1999). Similar to terrestrial deforestation, a damaged coral reef can take decades or centuries to recover. Reef building corals are extremely slow growing; most grow only 1-3cm per year (Harriott 1999; Carilli et al. 2010). Thus, it can take centuries for a colony with one meter diameter to grow. Massive and encrusting corals, which are generally the structural basis for a reef, grow even slower than branching corals (Morgan and Kench 2012). Coral growth rates are variable based on species, location, latitude, seasonal and local phenomena, but even the fastest growing corals will grow fewer than 10 centimeters per year (Morgan and Kench 2012). Corals are vital because they provide the three-dimensional structure upon which countless species depend (Graham et al. 2006; Graham and Nash 2013). There are many species, both vertebrate and invertebrate, that rely on live coral for at least one life stage. Many fish species rely on live coral for food and shelter (Cole et al. 2008; Coker et al. 2014; Emslie et al. 2014). In some cases, adult fish do not require live coral, but do so for food, shelter or recruitment at an earlier life stage. Thus, even though some adults do not require live coral, a lack of live coral can result in a decrease in abundance in some species (Feary et al. 2007; Wen et al. 2013). In

addition to those species that depend on live coral, there are numerous species that rely on the structure that corals provide on reefs for shelter or protection. After a coral senesces, the skeleton will remain on the reef for a period of time providing shelter and structure to those species that need it. The three-dimensional structure of a reef is also known as complexity, the physical environment that exists on that reef.

Reductions in coral cover as well as reef complexity showed more significant reductions in fish abundance than coral cover alone (Emslie et al. 2014). This indicates that it may take several years after bleaching events for the full effects to be evident among the fish community. Habitat degradation is one of the most devastating factors on coral reefs, responsible for declining populations, biodiversity loss and disruption of ecosystem service delivery (Feary et al. 2007). Coral bleaching is recently responsible for the majority of the habitat degradation on reefs in this region.

Due to numerous threats from overfishing, pollution and climate change, coral reefs are one of the most threatened ecosystems worldwide (Pratchett et al. 2014). One of the most devastating effects of global warming is that it can cause mass bleaching events due to rising ocean temperatures (Lough and Cantin 2014). The occurrence and extent of mass coral bleaching events has increased in frequency and intensity since the late 1990s. Coral bleaching is a natural stress response; it refers to breakdown of the symbiosis between the coral animal and their mutualistic algal symbiont due to the presence of a stressor. If the stressor persists for an extended period of time, it can lead to coral mortality. Mass bleaching events are occurring on every reef ecosystem worldwide (Sully et al. 2019). Bleaching events often lead to a decrease in coral cover

on a reef. A proxy for assessing the health of a coral reef is the metric ‘percent coral cover’ which provides an estimate for the amount of live coral present on a reef. Coral provides vital habitat for fish and invertebrates; the repercussions of coral bleaching include devastating short and long term effects on an ecosystem.

The El Niño-mediated bleaching event of 2015/2016 devastated many reefs around the globe and also those in the central and southern Red Sea, but the extent of mortality and further ecosystem repercussions have yet to be fully realized. While the link between an El Niño event and mass coral bleaching has been well documented (e.g., Bruno et al. 2001; Glynn et al. 2001; McClanahan et al. 2001; Baker et al. 2008; Elvan Ampou et al. 2017; Hughes et al. 2018), there is minimal literature on this topic focused on the Red Sea. In general, the Red Sea is understudied compared to other tropical regions of the world. There were reports of severe bleaching in the central Red Sea during the 2015/2016 worldwide mass coral bleaching event, which coincided with an El Niño (Monroe et al. 2018, in prep.; Genevier et al. 2019). In the Red Sea, El Niño events have been found to cause warmer winter water temperatures, which could limit the recovery potential from coral bleaching (Dasari et al. 2018).

### *1.3. Fisheries in the Red Sea*

There are two types of fisheries that contribute to the wild seafood supply in Saudi Arabia, large-scale commercial fisheries and small-scale artisanal fisheries, both of which are under-regulated. The artisanal fishery is responsible for the nearly 70% of the seafood production in the Saudi Arabian Red Sea (MOA Report, 2006; Jin et al.



2012). Artisanal fishers primarily use handlines, which account for 76% of their total landing. Gillnets and traps account for the majority of the remaining 24% of landings (MOA Report, 2006). The majority of the artisanal fishing effort is directed on or around coral reefs with fishers primarily targeting grouper, snapper, emperor, barracuda, jack, kingfish and tuna, depending on the time of year (Jin et al. 2012). The artisanal fishers generally have only one or two men per boat, and typically the boats return to port each night. The commercial fishery, however, employs a large boat with a crew that can stay out for days at a time. The larger scale commercial fisheries, which largely operate in the southern Red Sea, typically target mackerel, shrimp and squid, notably different from the artisanal fisheries (Jin et al. 2012). The commercial and artisanal fisheries both contribute to local fish markets. We focused our sampling on the Thuwal and Jeddah markets. Thuwal is a traditional fishing village, north of Jeddah. Because Jeddah is the largest city on the coast of the Red Sea, its demand for fresh fish is unrivaled. For these reasons, these two locations represent key fish markets in the kingdom. In addition to displaying which species are commonly removed from the Saudi reefs, the volume and prices of different species in the fish markets offer insight into what species fishers are landing and what consumers prefer.

While there is a wide range of species available at the fish market, high prices and high abundances of grouper species indicate a consumer preference for those species. Multi-gear fishing methods contribute to the high diversity of species present in local fish markets. Species range from small shrimp to large elasmobranchs and reef-associated species, including parrotfish and lobster. Studies have found that Saudi

Arabians prefer fish over other sources of protein (Khan et al. 2016; Moradi-Lakeh et al. 2016). Furthermore, 95-97% of Saudis eat fish regularly (Burger et al. 2014) and 25% of Saudi adults eat fish daily (Moradi-Lakeh et al. 2016). Due to the popularity of seafood coupled with a growing human population, the reefs in the Saudi Arabian Red Sea will continue to be fished at an unsustainable level, unless legislative action is taken (Jin et al. 2012).

Overfishing is occurring on a global scale, with the collapses of numerous fisheries in recent decades (Myers and Worm 2003). Despite minimal large-scale commercial fishing in the region (which in other parts of the world is often responsible for fisheries collapses), Saudi Arabia is not exempt from the global overfishing epidemic. It is estimated that Saudi Arabian reefs have been overfished since the early 1990s (Jin et al. 2012). Artisanal fisheries remove nearly 17,000MT annually from the Red Sea, with primary targets of top carnivores, including sharks and grouper, such as the highly prized “nagil” (*Plectropomus pessiliferus marisrubri*) (Myers et al. 2007). “Nagil” costs approximately 24 USD/kg. Due to the high price of “nagil”, fishers target this species heavily (Tsikliras and Polymeros 2014), which led to its overfished status in the Saudi Arabian Red Sea. The Sudanese side of the Red Sea, which features similar oceanographic and topographic conditions to the Saudi Arabian side of the Red Sea, possesses both larger individuals and a higher presence of these top carnivores. This discrepancy is likely the result of overfishing on the eastern coast the Red Sea (Kattan et al. 2017). Unfortunately, despite the awareness of the issue of overfishing worldwide, the issue persists in many regions, including Saudi Arabia.

While there are fishing regulations currently in place in the Saudi Arabian Red Sea, enforcement is limited. For example, despite a royal decree issued in 2008 which explicitly bans the catching and selling of sharks and other elasmobranch species, they are readily found in the Jeddah and Thuwal fish markets (Spaet and Berumen 2015). A large challenge facing marine policy is the lack of compliance with laws, often resulting from a lack of enforcement. The use of marine protected areas (MPA) as a management tool has been proven effective in maintaining biomass (Roberts and Polunin 1991; Côté et al. 2001) and their implementation has increased dramatically in recent years (Ban et al. 2017). The Saudi Arabian Red Sea has two marine protected areas in place, one in the Farasan Banks and one in the Al Wajh region. However due to limited enforcement, the MPAs are not functioning as “no take” areas, as they were designed (PERSGA, 2006). Thus, they are ineffective at protecting local biodiversity. In 1995 the Food and Agriculture Organization of the UN established the ‘Regional Organization for the Conservation of the Environment in the Red Sea and Gulf of Aden’ ( known as PERSGA) to try to maintain the high natural biodiversity in this region (PERSGA, 2006). PERSGA has proposed 75 MPAs in the Red Sea and Gulf of Aden region. Twelve of these have been implemented, two of which are in Saudi Arabia. However, PERSGA acknowledges that few of the MPAs are managed properly; the lack of surveillance and enforcement is common in the existing MPAs (PERSGA, 2006). Although these policies are designed to protect reef ecosystems, the lack of enforcement does little to protect these fragile ecosystems.

#### *1.4. Objectives*

Due to the culture in this area, with minimal reef-based tourism and a growing Saudi population, the provisioning service of harvest reef fish for food is the most vital one that coral reefs provide. The objective of this study was to determine how a coral bleaching event impacted potential fisheries revenue by using *in situ* fish survey biomass estimates and species-specific prices from local fish markets. It is important to understand how this service will be affected by future anthropogenic and climatic disturbances. By investigating the provisioning service at reefs with varying benthic states following a major bleaching event that significantly reduced coral cover, we can ascertain the flow-on effect to reef-based fisheries in this region. This can also provide insight into how future coral bleaching and mortality scenarios would impact local fishing.

## MATERIALS & METHODS

### 2.0. Focal Region

The Red Sea is a unique environment and relatively small body of water, only ~2000km in length and 355km wide at its widest point. Despite its small size, the oceanographic and physical characteristics vary greatly throughout the Red Sea, with temperature and salinity both decreasing with increasing latitude (Carvalho et al. 2019). To minimize potential variability associated with regional differences, this study focuses on the Farasan Banks region of the Red Sea, where the global bleaching

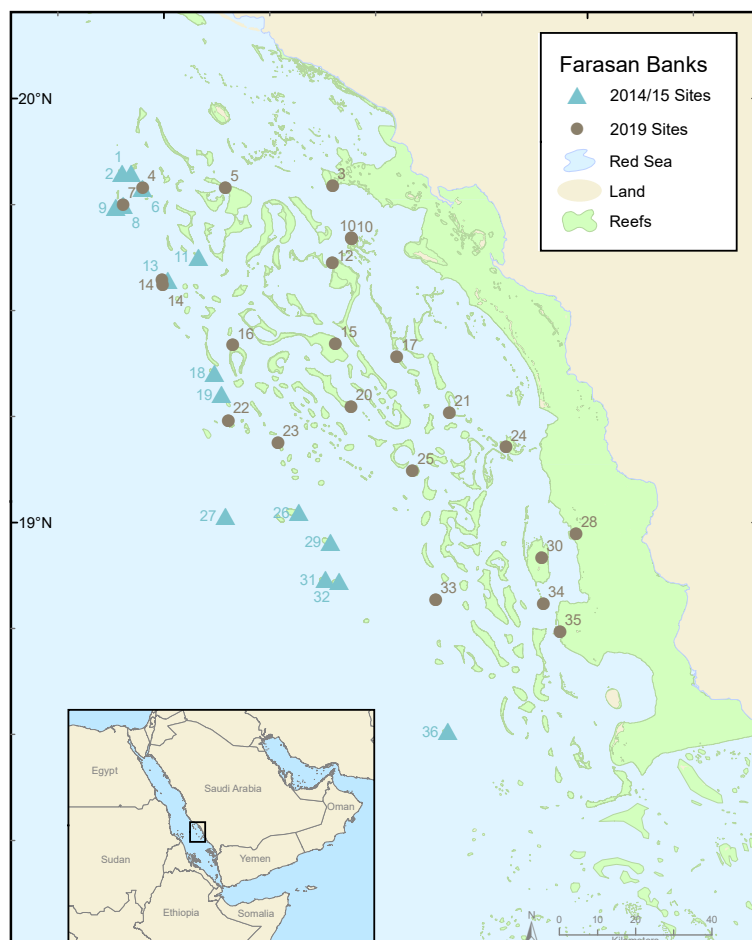


Figure 1. Map of the Farasan Banks region showing the locations of each survey site. Blue triangles indicate 2014/15 samples and brown circles indicate 2019 surveys. Map by Ute Langner.

event of 2015/16 triggered severe losses in coral cover. The northern end of the

Farasan Banks is at approximately 20°N, where the city of Al Lith is located and the southern end of the region approximately borders the city of Al Qunfudhah; both Al Lith and Al Qunfudhah are ports for artisanal fishing. This region of the Red Sea was found to have the most morphologically diverse reefs in the Red Sea (Rowlands et al. 2014). Due to the vast habitat diversity, both in complexity and reef structure, this area had been home to some of Saudi Arabia's best, most vibrant coral reefs (Bruckner and Dempsey 2015). With an estimated 6 million acres of coral reef, reaching up to 30 miles offshore, the Farasan Banks had been identified as a region of unusually high biodiversity and health (Bruckner and Dempsey 2015).

The Farasan Banks region was severely impacted by the global bleaching event in 2015-2016, as were most tropical regions worldwide (Hughes et al. 2017; Monroe et al. in prep.). The Red Sea experienced bleaching that began in the summer of 2015 and persisted until early 2016 (Monroe et al. 2018). Prior to this bleaching event, the Farasan Banks region had high levels of coral cover (with an average of 57% coral cover and some reefs as high as 86%) and diversity. After the bleaching event, some reefs in the Farasan Banks exhibited up to 90% declines in coral cover (Monroe et al. in prep.).

Reefs in this region were surveyed both before and after the bleaching event. Throughout 2014 and the spring of 2015 (before the bleaching event), 15 reefs were surveyed in the region: Al Jadir, As Saqhar, Belgium Point, Dohra, Dolphin Lagoon, Dorish Island, Labing Siyan Ka, Long Reef, Malathu, Mar Mar, Maras, Murabit Al Khail, Shakir, Shib Al Khatib and Shib Ammar (Figure 1). Between February and

May 2019, three and a half years after the bleaching event, 22 reefs in the region were surveyed: Abudefduf, Al Jadir, CP Reef, Dasaqiya, Dubarah, Freddy, Maktub, Malathu, Midshelf II, Minke, Miskah Island, Mur Abba, Nudibranch, Ribbon Reef, Shib Al Roab, Shib Aladeen, Shib Ammar, Shib As Sagah, Shib Dauqa, Sofia and Tartaruga (Figure 1). Unfortunately, because only three reefs sampled in 2014/15 were resampled in 2019, direct reef comparisons were not possible. All of the reefs sampled before the bleaching event were offshore reefs while the reefs sampled after the bleaching event ranged from offshore to inshore. A permutational multivariate analysis of variance (PERMANOVA) confirmed that the differences in fish community we saw after the bleaching event were not affected by the shelf position, i.e., fish communities on inshore, midshelf and offshore reefs could not be predicted by location on the shelf. Therefore, we assume that any changes between sampling before or after the bleaching event are a result of the bleaching event.

### *2.1. Ecosystem Services Assessment*

A key variable in managing fisheries effectively is knowing baseline landing information. For many regions of the world, this data is publicly and freely available. For example, all commercial fish landing data in the United States is available online from the National Oceanic and Atmospheric Administration (NOAA). An interactive webpage allows you to filter landings by year, state, species, weight and dollar value (<https://www.fisheries.noaa.gov/national/sustainable-fisheries/commercial-fisheries-landings>).

Similarly, the Common Fisheries Policy (CFP) of the European Union (EU) publishes

complementary data for all European Union fisheries landings ([https://ec.europa.eu/eurostat/statistics-explained/index.php/Fishery\\_statistics#Catches](https://ec.europa.eu/eurostat/statistics-explained/index.php/Fishery_statistics#Catches)). This data also includes fishery landing based on country and species and further describes trends from year to year. While many regions of the world offer public data on fisheries landings, there are also many regions for which no such data exists. Saudi Arabia is in the latter group; although there have been several attempts to reconstruct the catch based on various data sources (e.g., Tesfamichael and Pauly 2015). Therefore, in order to attain some baseline fisheries values, we surveyed local fish markets for abundance and price information.

Sampling local fish markets enabled us to collect up-to-date and accurate species-specific information on market values in the region. The most accurate method of valuing a provisioning service is through the use of direct market values (Sil et al. 2016; Ngoc 2018). Furthermore, the majority of the wild caught seafood in the region is not exported (MOA Report 2006). Therefore, direct market valuations are accurate estimates for the value of these fish. The largest proportion of Saudi Arabian artisanal fishermen are operating from within the Makkah region of the central Red Sea (Jeddah Facts and Figures 2017). The Jeddah and Thuwal fish markets are both located in this region. The locations of these markets also allowed us to sample both of them multiple times. The Jeddah and Thuwal fish markets were surveyed eleven times from February to August 2019. The Jeddah fish market was sampled nine times and the smaller Thuwal fish market was visited twice. Visits were both on weekdays and weekends and at various times of day in order to eliminate temporal bias. During each visit,



vendors were asked for the prices per kilogram of specific fish. If the vendor gave a price for the whole fish, the fish was also weighed to the nearest kilogram in order to calculate a price per kilogram. When the prices were posted, vendors were not interviewed, we simply collected the posted prices, to eliminate bias. Samplers were non-Arabic speakers; occasionally the language barrier prohibited interviews. This price information allowed us to calculate species-specific prices for each fish. Using this data from the fish market, combined with fish assemblage data collected from the reefs, we were able to calculate potential fisheries revenue for each reef.

#### *2.1.1. Determination of Price per Kilogram*

Upon each visit to the fish market, species-specific prices, as well as family level prices were recorded. Whether a species was assigned and mean price per family or specific species prices depended on both the number of individuals sampled and the similarity of that species to others in its family. Groupers are the most abundant group of fish at the fish market, therefore calculating prices for them was very important. Groupers are widely referred to as “hammour” in the fish market, therefore the prices obtained apply to many similar members of the Serranidae family. The species *Epinephelus summana*, *Plectropomus areolatus*, *Plectropomus pessuliferus marisrubri* and *Variola louti* are the only members of the Serranidae family given species-specific prices. These four species were given species-specific prices due to their high abundance or dissimilarity to other “hammour” species. *Epinephelus summana* was given species-specific prices because there were enough samples that an accurate

mean price could be calculated. *Plectropomus areolatus*, *P. pessuliferus marisrubri*, and *V. louti* are among the highest valued species at the markets. Although they are serranids, their prices are higher than the “hammour” price. Among the Lutjanidae family (snappers), *Lutjanus bohar* and *Macolor niger* were both given species-specific prices because their biology (size in particular) differs largely from other snappers. For the remaining snappers, two mean prices were calculated, one for “small snappers” and one for “large snappers”. Small snappers, which include (for the purposes of this study) *Lutjanus ehrenbergii* and *Lutjanus kasmira*, had a maximum size of 600mm or less. Large snappers, which include (for the purposes of this study) *Lutjanus argentimaculatus* and *Lutjanus sebae*, have a maximum size of over 600mm. Among the jacks, *Carangoides bajad* is the only species to have a species-specific price because there were enough samples to calculate a mean price. The prices for the rest of the jacks were averaged. Because there is very little species discrimination at the markets between Lethrinidae species (emperors), all species were assigned a composite price. Most members of the Scaridae family (parrotfishes) were given mean prices due to their similarities and lack of distinction at the fish market. However, *B. muicatum* and *C. bicolor* were however given species-specific prices due to their uniqueness and price discrepancy from other members of the family.

### 2.1.2. Fisheries Valuations

Using the biomass calculations (tonnes/hectare) and the species-specific prices, we were able to calculate the potential fisheries revenue (USD/hectare) from each reef

before and after the bleaching event. We compared those values to determine if a change occurred after the bleaching event. Because the data did not meet assumptions of normal distribution (tested using a Shapiro-Wilk test) and equal variances required to perform a t-test, we used the non-parametric Mann-Whitney U Test (Wilcoxon rank sum test) to determine if there was a significant difference between the valuations before and after the bleaching event.

## ***2.2. Reef Degradation Assessment***

### *2.2.1 Benthic Survey Methodology*

Coral reefs are one of the most heavily studied ecosystems in marine science, particularly with the threats from anthropogenic global change (Hoegh-Guldberg and Bruno 2010). There are a myriad of techniques used to measure the health of coral reefs, ranging from the use of remotely sensed satellite data to *in situ* coral colony size measurements (e.g., Dustan et al. 2013; Bozec et al. 2015; Ferrari et al. 2016). As anthropogenic stressors are expected to continue to increase, the necessity for efficient and accurate monitoring techniques is paramount (Ferrari et al. 2016). Several studies have found links between the benthic condition of a coral reef and its respective fish community (Luckhurst and Luckhurst 1978; McCormick 1994; Kuffner et al. 2007; Wismer et al. 2009; Dustan et al. 2013; Graham and Nash 2013; Pratchett et al. 2014). Therefore, in addition to fish community assessments, benthic parameters were measured at each site.

An important parameter of coral reef health is the amount of live scleractinian (reef-building) coral, which can be measured using the point intercept method. This is a time efficient and accurate method of assessing the benthic cover on a reef (Facon et al. 2016). In 2019, fifty benthic photos were taken along each transect, one at each meter. The photos were taken using an Olympus TG5 or a Canon G7x. The photos were then analyzed using the point intercept method, the center of each photo was classified as either: soft coral, sand, pavement, rubble, live hard coral, dead hard coral, turf algae, algae, or other. This method was used to simulate the same method used in 2014/2015, when point intercept surveys were conducted in the field. At each meter along the transect, the substrate just below the meter mark was placed into one of the same categories as above, resulting in a total 50 points per transect. For general benthic condition assessments, the point intercept method is one of the most common, accurate and time efficient methods of estimating coral cover (Wismer et al. 2009; Facon et al. 2016). The point intercept method is as accurate as other methods and takes considerably less time (Facon et al. 2016).

In addition to coral cover, other metrics are important indicators of reef health. Rugosity is a measure of the physical complexity of the reef. Live coral provides shelter for many species, however the skeleton of a dead scleractinian coral can provide structure for a period of time after the coral itself senesces. The reef rugosity index is the ratio of a straight transect line to the distance a flexible chain covers when draped over the reef substrate (Dustan et al. 2013). A lower value indicates a less complex reef and a high value indicates in more complex reef. Due to the link

between rugosity and fish communities (Luckhurst and Luckhurst 1978; Kuffner et al. 2007; Rogers et al. 2017), we also measured rugosity at each reef in 2019. Because the chain and tape method of measuring rugosity is the most time efficient, accurate and commonly used (e.g., Knudby and LeDrew 2007; Kuffner et al. 2007; Young et al. 2018; Dustan et al. 2013; Bozec et al. 2015) we measured rugosity using this method. At three points along each replicate transect (nine times per reef), rugosity measurements are taken using a 5.6m chain draped along the three-dimensional topography of the reef. The two-dimensional distance from the beginning to the end of the chain is then measured and the rugosity is calculated using the formula  $R=l/d$ , where  $R$  is the rugosity,  $l$  is the total linear length of the chain and  $d$  is the horizontal distance covered by the chain following the reef contour, with higher values indicating more complexity (Luckhurst and Luckhurst 1978). Due to sampling limitations, rugosity measurements were only taken in 2019, not in 2014/15.

### 2.2.2. Fish Survey Methodology

*In situ* field surveys assessed the fish communities at each reef using the underwater visual census (UVC) method, a common method used to estimate fish community structure (e.g., Friedlander and Parrish 1998; Ruttenberg et al. 2011; Williams et al. 2011; Kattan et al. 2017; Anderson et al. 2019). First described in 1954, UVC is a non-destructive method of documenting important fish community demographics in fish, including species, number and size of individuals (Brock 1954). When the UVC is conducted along a belt transect of known length, the parameters

recorded during the survey can be used to estimate biomass. The UVC technique has become one of the most widely used techniques for estimating biomass for many reasons; it is a cost and time effective method that can be replicated quickly without removing physical specimens from the area (Sale and Douglas 1981; Cheal and Thompson 1997). Other methods include the roving diver UVC method, as well as destructive methods including the use of clove oil or rotenone, seine netting and others to estimate reef fish assemblages (Sale and Douglas 1981; R. E. Brock 1982; Schmitt et al. 2002; Coker et al. 2017). The roving diver UVC technique can potentially document a larger number of species on a given reef than belt UVC methods, however due to the inconsistent area covered, biomass estimates are difficult to accurately estimate (Schmitt et al. 2002). Most other methods to estimate biomass of fish species on a given reef involve removing the fish from the reef through the use of chemicals or netting. These methods are much more detrimental to the reef and cannot be replicated as quickly (Almany 2004; Coker et al. 2017). Each method to assess fish communities has its own limitations. One of the main limitations to UVC belt transects is that cryptic and nocturnal species are often underestimated (Schmitt et al. 2002). As each survey method has different strengths and weaknesses, the best survey method depends on the aims of the specific study (Coker et al. 2017). For the purposes of this study, assessing these fish assemblages from a fisheries perspective, where larger, diurnally active species are most important, the UVC with a belt transect is the best option. Underwater visual census using belt transects provide all the information needed to calculate biomass for specific species on specific reefs. Furthermore, using

UVC allows us to compare data collected in 2019 with data collected in 2014 and 2015 as any limitations and biases are the same for all sampling periods.

At each site, three replicate transects were conducted at a depth of 10m. As a surveyor swims along the transect, he or she documents the species, individual size and count of each species along the transect. When there was a current present, the surveys were conducted while swimming against the current. The surveys conducted in 2014 and 2015, prior to the bleaching event, employed 25m replicates. The surveys conducted in 2019, three and a half years after the bleaching event, utilized 50m replicates. Differences in relative count totals due to differing transect lengths were eliminated by conducting all analyses using biomass, measured in tonnes per hectare. In order to minimize bias, one surveyor conducted all of the 2014/15 surveys and one surveyor conducted all of the 2019 surveys. Most conspicuous diurnally active fish with a total length of  $>3\text{cm}$  was recorded. Large bodied species, with a total length  $>20\text{cm}$ , were recorded when within 4m on either side of the transect (8m total width) small bodied species were recorded when within 2m on either side of the transect (4m total width); this combination of transect widths are in accord with other similar studies (Sandin et al. 2008; Kattan et al. 2017). This technique maximizes accuracy and minimizes bias (Mapstone and Ayling 1998). In order to minimize the disruption to the fish, the transect tape was laid by a second diver, following immediately behind the surveyor. This transect tape was used to conduct the subsequent benthic surveys.

### ***2.3. Assessing Fisheries in the Red Sea***

#### ***2.3.1. Fish Market Surveys***

In order to assess species composition to better understand which species are being heavily targeted and removed from local reefs, three trips were made to the Jeddah fish market. During each visit, we counted, identified and measured the total length of every fish on display from 15-20 of the Red Sea stalls in the market. Unfortunately, due to time limitations we were unable to survey every Red Sea vendor. The Jeddah fish market sells locally caught fish, imported fish and farmed fish. Based on the species, quantities and display, we can determine if the species were likely locally caught or not. We sampled for one hour and identified, counted and measured as many fish as possible. Each survey was conducted between 0900 and 1200. Generally, the vendors at the fish market are not fishermen themselves, the fish are sold wholesale at auction around 0500-0600, where vendors purchase them to sell retail. We surveyed the retail prices only. Additionally, we only included fish that were on display when we visited each vendor, any fish that were in coolers or freezers were not sampled. After each visit, using the total number of samples and the quantity for each family, we calculated relative abundances in the fish market.

Because we were not able to sample the entire fish market, all comparisons were made using percentages of the total individuals sampled. The percent by count was calculated for each family: Serranidae, Lutjanidae, Carangidae, Lethrinidae, Labridae, Scarinae (Labridae). Using the lengths recorded for each individual, a mass was calculated using known length weight estimates and the formula:  $W = a \times L^b$ , where  $W$  represents the weight in grams,  $L$  represents total length in centimeters and  $a$  and  $b$  are species specific constants obtained from FishBase (Friedlander and



DeMartini 2002; Froese and Pauly 2014). We then calculated percentages by biomass of the five families. Because biomass is not comparable between the reefs and fish market, we could only compare the community using relative abundances of species and groups. Lastly, using the biomass coupled with collected prices, we calculated which families generate the most revenue for the reef-based fishery. The weight of the fish, multiplied by the price per kilogram gives us a price for the fish, and the summation of all those values yields the total potential revenue. Because we did not sample the entire market, we again used comparisons of percentages to assess the fish market revenues.

### *2.3.2. Selection of Focal Species*

Although a large number of species was sampled in the reef surveys, only species deemed “fisheries relevant” were included in our analyses. All species that were sampled during the fish market surveys were included. Additional species were included because of their presence in a report published by the Saudi Arabian Ministry of Agriculture (MOA) (MOA Report 2006), which lists the reported catches of commercial and artisanal fisheries, broken down by region and group. Groups with a four-year sum landing of less than 10MT were excluded from our analyses because those species are likely not highly targeted or highly valued species. Examples of these excluded fish include filefishes, goatfishes, triggerfishes and angelfishes. While relatively common on the reefs, they are not found in high abundance in the markets. According to the MOA report, the wrasse family was responsible for a cumulative

landing of 106MT between 2003 and 2006. However, the wrasse family is extraordinarily diverse; Red Sea species range in size from a maximum length of 6cm (*Minilabrus striatus*) to a maximum length of 230cm (*Cheilinus undulates*) (Lieske and Myers 2004; NB: the MOA report treats parrotfishes as a separate family). In order to account for this diversity, only wrasse species with a maximum length of 20cm or larger were included in our analysis. Smaller wrasse species are not highly abundant in the markets and thus would have too small a fisheries value to be relevant. Surgeonfishes and unicornfishes made up 456MT between 2003 and 2006. Although one species of unicornfish (*Naso hexacanthus*), is relatively abundant on the reefs, it was removed from the study because it was never recorded in the fish markets and due to its biology, it is not catchable by a traditional hook and line, the primary method of fishing in this region. *Caesio* spp., *Barracuda genie*. and *Elagatis bipinnulata* were not included in the data analysis because, although they are seen on reefs, they do not rely on the reefs and often traverse between reefs. Because these species do not necessarily associate with reefs, including them in our price calculations would lead to overestimations of valuations.

### 2.3.3. Benthic Cover Analysis

We conducted a principal component analysis (PCA) to investigate the shift in benthic cover before and after the bleaching event. In order to visualize the data, we plotted the PCA results using RStudio (Version 1.1.456, ggplot2 package). This data did not meet the assumptions required for parametric tests, so we conducted the non-

parametric PERMANOVA to determine if there was a significant difference between the benthic composition before and after the bleaching event. The PERMANOVA was conducted using the `adonis` command in the `vegan` package.

Although we do not have rugosity measurements from before the bleaching event, we investigated the relationship between coral cover and rugosity among the reefs in 2019. Using the Shapiro-Wilk test, we determined that the coral cover data is not normally distributed although the rugosity data was normally distributed. Therefore, we used the non-parametric Spearman's rank correlation coefficient to determine if there is a correlation between the coral cover and rugosity. In order to determine if there was a correlation between the shelf position and rugosity, we conducted Kruskal Wallis rank sum tests.

#### *2.3.4. Fish Community Analysis*

There are many benefits to conducting calculations on biomass values. In general, biomass values allow us to have an idea what the entire reef fish assemblage looks like, however we only focused on a subset of the reef fish community. For this study, they allow us to compare values between different fisheries relevant species and easily compare to fish market data. Additionally, due to the variation in sampling technique, where the fish surveys from before the bleaching event employed 25m transects, but after the bleaching event used 50m transects, we could not use simple count data for our analyses because that would have likely led to increases in many species due to the larger sample area. Biomass calculations allow us to standardize the

dataset. Additionally, biomass data can be more informative about the community as a whole, particularly when looking from a fisheries or economic perspective. The biomass is far more informative than a simple count. Biomass is a commonly used metric for assessing changes in fish community (e.g., Graham et al. 2007; Kattan et al. 2017). By recording the lengths of the fish on each transect, we were able to calculate the biomass using published Bayesian length-weight relationships from FishBase with the formula:  $W = a \times L^b$ , where  $W$  represents the weight in grams,  $L$  represents total length in centimeters and  $a$  and  $b$  are species specific constants (Froese and Pauly 2014). For the few species that did not have published Bayesian length-weight values, we used values from a fish with a similar body shape to calculate biomass. All study species were recorded in 50mm size classes from 10cm to 40cm, then in 100mm size classes up to 150cm (i.e. our size bins were >100mm, 100-149, 150-199, 200-249, 250-299, 300-349, 350-399, 400-499, 500-599, 600-699, 700-799, 800-999, 1000-1499, 1500+). For each species on each reef, we calculated a biomass estimate (tonnes/hectare).

After calculating biomass values for each study species on each reef, all statistical analyses were conducted using those values. In order to minimize the effects of extremely abundant species, we square-root transformed our data (following Shedrawi et al. 2014). All analyses were conducted using R, in RStudio (Version 1.1.456). We used the meta.MDS function from the vegan packages to calculate MDS values from the biomass data. Using those values we created a Non-Metric Multidimensional Scaling (nMDS) plot to assess the differences between sites and

years. Our data failed the Shapiro-Wilk normality test and the Levene's test for homogeneity of variance, so we used the non-parametric PERMANOVA to determine if our results were significant. The PERMANOVA was conducted using the `adonis` command in the `vegan` package. If the results were significant, we used a similarity percentage analysis (SIMPER) to determine which species were contributing the most to assess changes in fish community between the reefs before and after the bleaching event. To test for correlations between fish species parameters (biomass, abundance, species richness, price) and benthic cover parameters (coral cover, rugosity), we conducted Spearman rank-order correlations. Because all of the data, with the exception of the rugosity data, was not normally distributed, we used the non-parametric PERMANOVA to investigate the links between these factors.

## RESULTS

### ***3.1. Ecosystem Services Valuation***

#### ***3.1.1. Reef Valuations***

There was a large variance among the values per reef from both before and after the bleaching event. The lowest value per reef before the bleaching event was found at Mar Mar, yielding 3,647 USD/hectare. The most highly valued reef from before the bleaching event was Dolphin Lagoon with a value of 27,596 USD/hectare. The lowest valued reef from after the bleaching event was Maktub, with a mean value of 1,859 USD/hectare, less than the lowest valued reef from before the bleaching event (Table 3). The reef with the highest value after the bleaching event was Malathu, with a value of 21,416 USD/hectare, lower than the highest valued reef from before the bleaching event. The mean value per reef before the bleaching event was 7,913 USD/hectare, the mean value per reef after the bleaching event was 6,814 USD/hectare. There was a slight decrease in the mean value per reef, after the bleaching event, however a Mann-Whitney U Test failed to detect a significant difference ( $p=0.8$ ).

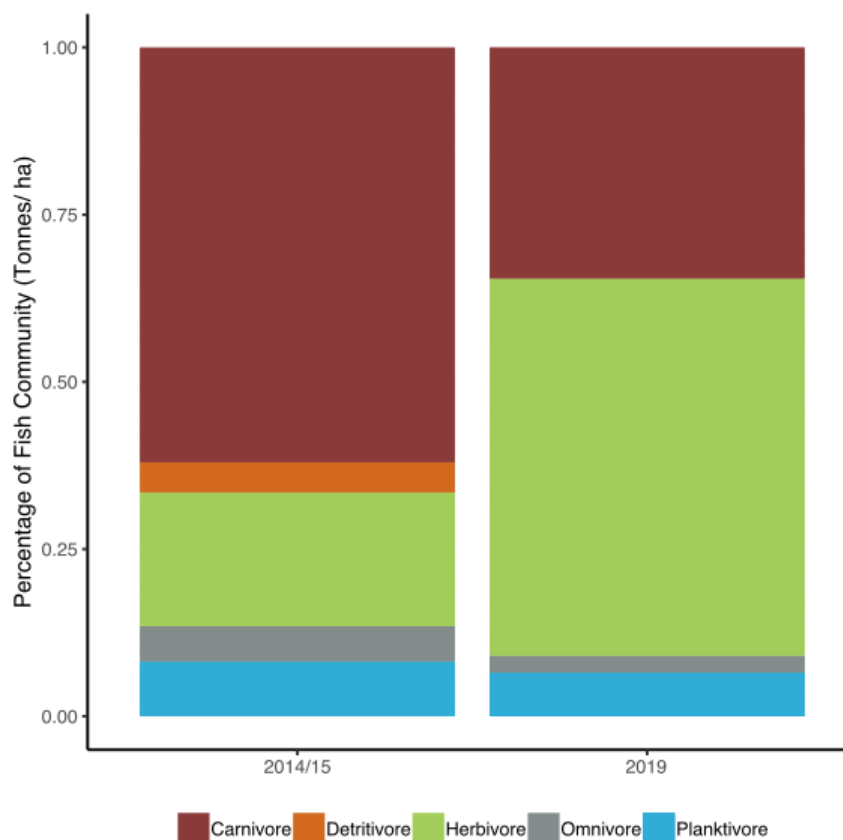


Figure 2. Stacked bar plot displaying the relative percentages of the sampled fish communities that are carnivores (red), detritivores (orange), herbivores, omnivores (grey) and planktivores (blue) before and after the 2015 bleaching event. An increase in herbivorous species and decrease in carnivorous species are apparent.

While there was not a statistically significant change in the total value for each reef, there was a change in the composition of the total value of the reef, (i.e. the species on the reef have changed while the overall reef value did not). Prior to the bleaching event, reefs had an average value of 7,913 USD/hectare, not significantly different from the slightly larger average value after the bleaching event of 6,814 USD/hectare. Notably, prior to the 2015-2016 bleaching event, the fish community was nearly 70% carnivores, which are more highly valued in the markets, while herbivores represented approximately 25% of the fish community (Figure 2).

However, after the bleaching event, the carnivores represented only about 25% of the total community and herbivores represented more than 50% of the assemblage (Figure 2).

Table 2. Table showing the mean value ( $\pm$  SE) of each reef (USD/ hectare) before (2014/15; left) and after (2019; right) the bleaching event.

2014/15		2019	
Reef	USD / hectare		USD / hectare
Dolphin Lagoon	\$27,596 $\pm$ 7,250	Malathu	\$21,416 $\pm$ 6,790
Dohra	\$10,572 $\pm$ 3,023	Tartaruga	\$17,774 $\pm$ 9,201
Al Jadir	\$10,489 $\pm$ 4,538	Shib Aladeen	\$13,644 $\pm$ 2,111
Murabit Al Khail	\$9,491 $\pm$ 2,838	Shib Dauqa	\$13,526 $\pm$ 1,490
As Saqhar	\$8,207 $\pm$ 444	Abudefduf	\$11,396 $\pm$ 3,522
Shakir	\$7,650 $\pm$ 3,932	Miskah Island	\$8,814 $\pm$ 1,654
Labing Siyan	\$7,616 $\pm$ 3,954	Shib Ammar	\$5,693 $\pm$ 1,855
Shib Al Khatib	\$7,393 $\pm$ 1,169	Midshelf II	\$5,375 $\pm$ 1,117
Shib Ammar	\$6,822 $\pm$ 1,367	Dasaqiya	\$5,273 $\pm$ 1,276
Dorish Island	\$6,367 $\pm$ 868	Sofia	\$5,069 $\pm$ 1,449
Maras	\$4,923 $\pm$ 1,479	Shib al Roab	\$4,233 $\pm$ 1,394
Belgium Point	\$4,012 $\pm$ 348	Minke	\$4,071 $\pm$ 442
Malathu	\$3,911 $\pm$ 301	Al Jadir	\$3,837 $\pm$ 216
Mar Mar	\$3,647 $\pm$ 1,455	Freddy	\$3,741 $\pm$ 1,894
Long Reef	\$2,581 $\pm$ 144	Dubarah	\$3,715 $\pm$ 592
		CP Reef	\$3,714 $\pm$ 205
Average $\pm$ SE	\$7,913 $\pm$ 1,524	Ribbon	\$3,423 $\pm$ 257
		Nudibranch	\$2,311 $\pm$ 459
		Shib As Sagah	\$2,250 $\pm$ 186
		Mur Abba	\$1,961 $\pm$ 272
		Maktub	\$1,859 $\pm$ 628
		Average $\pm$ SE	\$6,814 $\pm$ 1,177

### 3.2. Assessment of Reef Degradation

#### 3.2.1. Benthic Cover

There was a significant shift in the benthic composition of the Farasan Banks reefs before and after the bleaching event. The results of our PCA highlight the differences between the two groups (Figure 3). There is clear separation between the two clusters; the 2014/15 reefs group tightly on the right side of the plot while the



2019 reefs group more broadly on the left side of the plot. The separation is primarily driven by PC1, which is responsible for 33.21% of the variation in the data. The primary variables affecting PC1 are live hard coral (PC1 loading: 0.464) and live soft coral (PC1 loading: 0.463); the 2014/15 reefs strongly associate with those variables. Benthic characteristics including dead hard coral, rubble and algae, which are all indications of a degrading reef, cluster together on the left side of the PCA plot, where the reefs from after the bleaching event cluster. Benthic characteristics such as macroalgae, rubble and dead hard coral characterize the reefs on the left side of the plot, indicative of the reefs after the bleaching event. A PERMANOVA confirmed that there was a significant difference in the benthic cover before the bleaching event compared to after ( $F=97.227$ ,  $p=0.001$ ).

As of 2019, there was no correlation between the coral cover on a reef and the physical complexity of that reef. This was confirmed by the Spearman's rank correlation coefficient failing to detect a significant association between the two ( $p=0.97$ ). Among inshore, midshelf and offshore reefs there is a wide range of rugosity measurements. The lowest rugosity measurement, 1.31, came from Dasaqiya, a midshelf reef, however, the highest rugosity value was recorded at Shib Aladeen, another midshelf reef, with a rugosity value of 2.23. The Kruskal-Wallis rank sum test which we used to investigate the relationship between shelf position and rugosity, also did not find a significant relationship between the two ( $p=0.39$ ).

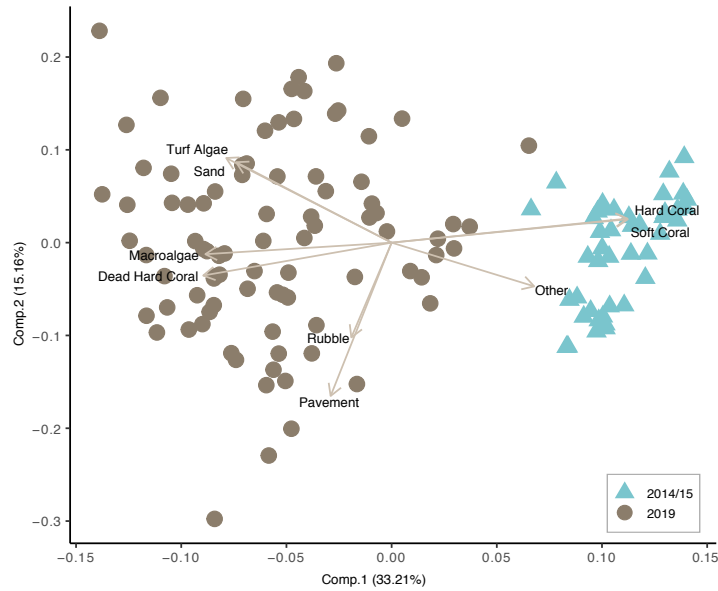


Figure 3. A principal component analysis (PCA) of benthic composition be 2014/15 (blue triangles) and in 2019 (brown circles). Gray arrows represent the direction and intensity of variables responsible for changes in benthic community. PC1 is responsible for 33.21% of the variation. PC2 is responsible for 15.1% of the variation.

### 3.2.2. Fish Community

Our results indicate that there is a significant difference between the fish assemblages before compared to after the bleaching event. We first used an nMDS to visualize distinctions between the two groups (Figure 4). Although some overlap is present in the nMDS plot, there is general clustering of the 2014/15 reefs on the right side of the plot, and the 2019 reefs on the left side of the plot (Figure 5). A PERMANOVA confirmed the significant difference between the two fish communities ( $F=4.3289$ ,  $p=0.003$ ). Furthermore, the SIMPER analysis identified *Chlorurus sordidus*, *Scarus niger*, *Naso elegans*, *Ctenochaetus striatus*, *Scarus ferrugineus*, *Acanthurus gahhm*, *Monotaxis grandoculis*, *Macolor niger*,

*Cephalopholis miniata*, *Naso unicornis*, *Lutjanus kasmira*, *Lutjanus bohar* and *Cetoscarus bicolor* driving the differences between the communities before and after the bleaching event. Those 13 species are responsible for more than 50% of the variation between the communities. The four species which increased the most were *S. niger*, *N. elegans*, *S. ferrugineus* and *S. chlorurus*, all herbivorous species (Figure 5). The species that declined the most were *M. grandoculis* and *C. ignobilis*.

Using the Spearman rank-order correlation, we found a significant correlation between coral cover and biomass ( $p=0.002$ ), coral cover and species richness ( $p=0.002$ ) and a correlation between coral cover and value per reef ( $p=0.042$ ; Figure 6). We did not find significant correlations between rugosity and biomass ( $p=0.87$ ) or abundance ( $p=0.84$ ) or species richness ( $p=0.45$ ).

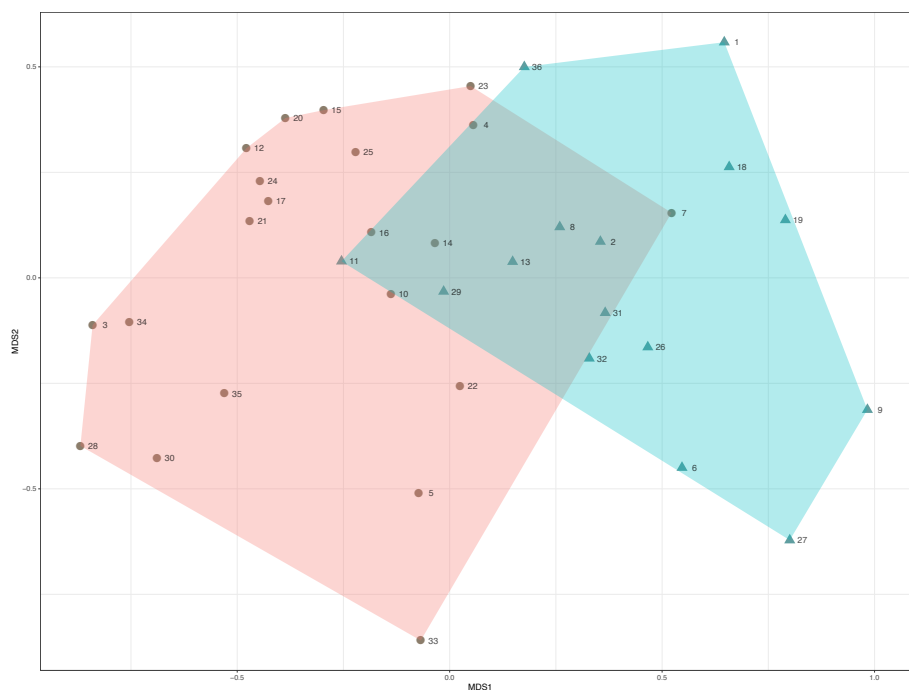


Figure 4. Non-Metric Multidimensional Scaling (NMDS) plot showing the fish communities before (light blue triangles) and after (brown circles) the 2015 bleaching event. Reefs are numbered according to decreasing latitude.

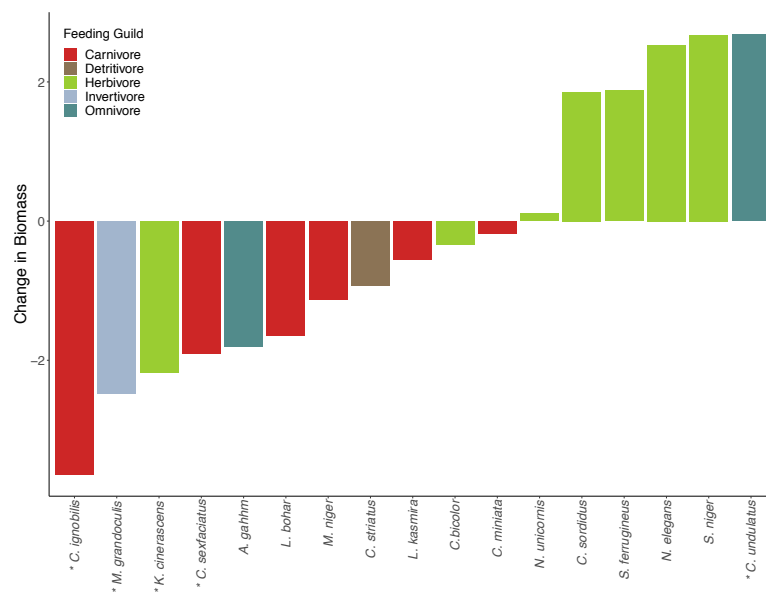


Figure 5. Barplot showing the changes in absolute biomass of the 14 most influential species according to the SIMPER analysis and an additional five species (denoted with \*) that exhibited large changes in biomass before compared to after the bleaching event. Red indicate carnivorous species, brown indicates detritivores, green represents herbivores, silver represents invertivores and teal represents omnivores.

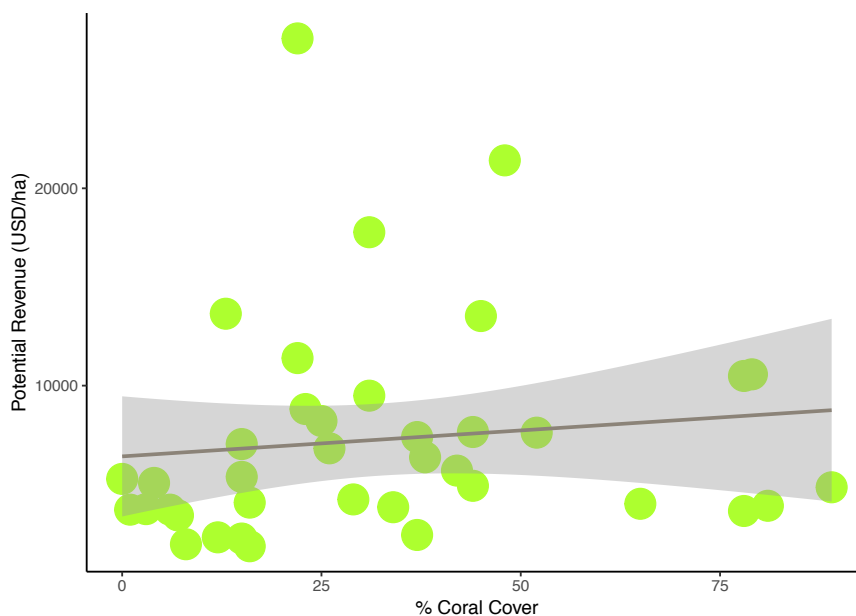


Figure 6. A spearman rank correlation detected a significant correlation between coral cover and potential revenue per reef, inclusive of reefs before and after the bleaching event.

The species with greatest increases in biomass after the bleaching event were *N. elegans*, *S. niger*, *C. undulatus*, *S. ferrugineus* and *C. sordidus*. Four of those species were identified by the SIMPER analysis as contributing significantly to the changes between the fish communities. Additionally, those species are all herbivores with the exception of *C. undulatus* which is an invertivore. The species with the lowest overall changes in biomass were *C. oligosticta*, *S. luridus*, *C. abudjubbe*, *G. caeruleus*, and *V. louti*. *Cephalopholis oligosticta* and *V. louti* are carnivores, *S. luridus* is an herbivore and *C. abudjubbe* and *G. caeruleus* are invertivores. The five species with the greatest declines in biomass were: *S. genie*, *C. ignobilis*, *K. cinerascens*, *M. grandoculis* and *C. sexfaciatus*, all of which are carnivores with the exceptions of *K. cinerascens*, an herbivore.

### ***3.3. Fisheries in Saudi Arabia***

#### ***3.3.1. Fish Market***

A total of 3,036 fish were counted at the Jeddah fish market. Collectively, grouper species had the greatest count (1,085) of individuals making up 36% of the total count in the market. Among the 3,036 fish we sampled at the Jeddah fish market, 55% of the potential revenue comes from serranids. The second most abundant group was the emperors, of which 700 were counted resulting in 23% of the total market count. Emperors account for 16% of the total biomass and 11% of the potential revenue. Following emperors, parrotfishes were the next most abundant by count, 14% of the total at the market (421 individuals). Parrotfishes represent 16% of the total biomass and 14% of the potential revenue. There were 189 jacks and 171 snappers recorded, each making up another 6% of the total abundance at the fish market. Jacks account for 6% of the total individuals, 4% of the biomass and only 3% of the potential revenue. Snappers represent 6% of the individuals, 9% of the biomass and 5% of the potential revenue. Although only 62 wrasses were counted, 2% of the total individuals and 5% of the total biomass, they account for 10% of the potential revenue. The remaining 408 individuals, which include surgeonfish, unicornfish, spadefish, barracuda and others, were grouped together to generate the remaining 13% of individuals, yet only 4% of the total biomass and 2% of the potential revenue (Figure 7).

There is variation among the biomass, count and potential revenue from the fish market data, however there is far greater variation between the fish market values

and the reef values. Among the fish market data, groupers, emperors and parrotfishes are always the highest proportions, of biomass, count and potential revenue.

Conversely, from the reefs before the bleaching event, groupers are one of the smallest groups by biomass. From before the bleaching event to after, there was limited change between the snappers, wrasse and emperors. The jacks decreased from 13% of the assemblage to just 2%. The parrotfishes increased from 9.7% of the total biomass to 35% of the total biomass. Grouper species also increased from 7.5% to 15% which was largely made up of *C. miniata* and *C. hemistiktos*, smaller grouper species.

There is a discrepancy between the fish that are most abundant in the fish market and those that are most abundant on the reefs. Species that are abundant in the fish market, such as *P. pessuliferus marisrubri*, *P. areolatus* and *E. summana* are far less abundant on the reefs. Species including *H. harid* and *N. unicornis* are very abundant on the reefs and often in low abundance at the fish market.

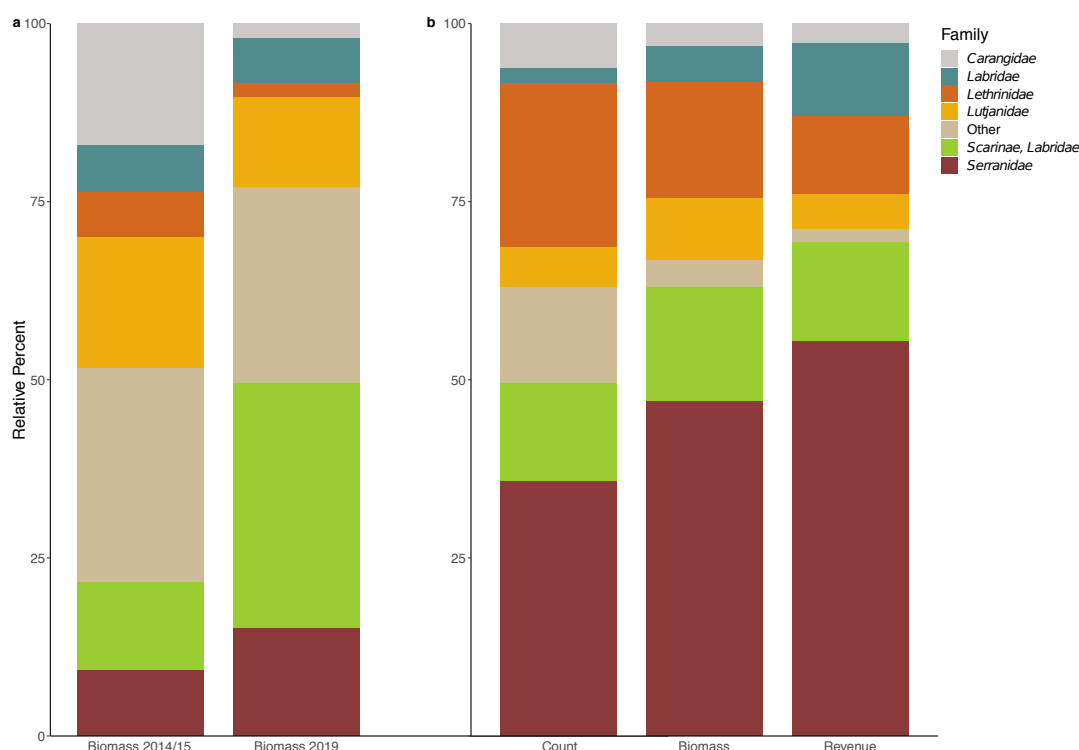


Figure 7. **a.** Results from reef surveys, relative percent of the total biomass of Carangidae, Labridae, Lethrinidae, Lutjanidae, Scarinae and Serranidae. Surveys from 2014/15 are on the left, 2019 on the right, exhibiting a notable increase in Scarinae and decrease in Carangidae. **b.** Results from the fish market surveys, the percent of the total count of individuals, total biomass and total potential revenue sampled in the market, broken down by family.

Table 3. The average price per kilogram  $\pm$  SE (USD/kg), average size  $\pm$  SE (mm), and proportion of occurrence of key fisheries species sampled at central Red Sea fish markets. Prices denoted with \* indicate a species-specific price, where all others are averaged to the family level. Proportion of occurrence was calculated by dividing the total number of that species by the total number of individuals sampled.

Species	Family	Price/kg (USD)	Average Size (mm)	Proportion of Occurrence
<i>Lutjanus kasmira</i>	Lutjanidae	\$5.51 $\pm$ 0.7	200.0 $\pm$ 0.0	1.1%
<i>Cheilinus abudjubbe</i>	Labridae	\$6.41 $\pm$ 0.6 *	271.9 $\pm$ 10.2	0.5%
<i>Siganus rivulatus</i>	Siganidae	\$7.09 $\pm$ 1.5	177.8 $\pm$ 2.6	3.0%
<i>Naso unicornis</i>	Acanthuridae	\$8.10 $\pm$ 1.11	400.0 $\pm$ 0.0	0.2%
<i>Gymnocranius grandoculis</i>	Lethrinidae	\$8.10 $\pm$ 1.2	520.6 $\pm$ 14.3	1.1%
<i>Lethrinus harak</i>	Lethrinidae	\$8.10 $\pm$ 1.2	350.0 $\pm$ 0.0	0.2%
<i>Lethrinus mahsena</i>	Lethrinidae	\$8.10 $\pm$ 1.2	289.0 $\pm$ 3.7	9.6%
<i>Monotaxis grandoculis</i>	Lethrinidae	\$8.10 $\pm$ 1.5	313.6 $\pm$ 6.7	0.4%
<i>Lutjanus argentimaculatus</i>	Lutjanidae	\$8.55 $\pm$ 1.0	618.2 $\pm$ 25.1	0.4%
<i>Lutjanus bohar</i>	Lutjanidae	\$8.55 $\pm$ 1.0	425.0 $\pm$ 113.9	0.1%
<i>Macolor niger</i>	Lutjanidae	\$8.55 $\pm$ 1.0	433.3 $\pm$ 19.2	0.2%



<i>Bolbometapon muricatum</i>	Scarinae, Labridae	\$10.38 ± 0.7	825 ± 54.5	0.1%
<i>Caranx ignobilis</i>	Carangidae	\$9.74 ± 1.1	700 ± 124.7	0.1%
<i>Caranx melampygus</i>	Carangidae	\$9.74 ± 1.2	287.5 ± 17.3	0.9%
<i>Caranx sexfaciatus</i>	Carangidae	\$9.74 ± 1.3	250.0 ± 0.0	0.2%
<i>Chlorurus sordidus</i>	Scarinae, Labridae	\$10.38 ± 0.7	368.2 ± 5.1	0.0%
<i>Hipposcarus harid</i>	Scarinae, Labridae	\$10.38 ± 0.7	268.2 ± 9.5	0.0%
<i>Scarus ferrugineus</i>	Scarinae, Labridae	\$10.38 ± 0.7	316.0 ± 6.0	3.4%
<i>Scarus ghobban</i>	Scarinae, Labridae	\$10.38 ± 0.7	500.0 ± 18.2	0.9%
<i>Scarus niger</i>	Scarinae, Labridae	\$10.38 ± 0.7	350.0 ± 0.0	0.3%
<i>Cephalopholis hemistiktos</i>	Serranidae	\$11.18 ± 0.7	150.0 ± 0.0	0.0%
<i>Cephalopholis miniata</i>	Serranidae	\$11.18 ± 0.7	290.0 ± 21.9	0.2%
<i>Cephalopholis oligosticta</i>	Serranidae	\$11.18 ± 0.7	344.2 ± 4.1	0.9%
<i>Cephalopholis sexmaculata</i>	Serranidae	\$11.18 ± 0.7	250.0 ± 0.0	0.7%
<i>Cephalopholis sonnerati</i>	Serranidae	\$11.18 ± 0.7	311.7 ± 6.2	3.8%
<i>Epinephelus chlorostigma</i>	Serranidae	\$11.18 ± 0.7	403.9 ± 10.4	5.9%
<i>Epinephelus fuscoguttatus</i>	Serranidae	\$11.18 ± 0.7	550.0 ± 25.0	0.1%
<i>Epinephelus malabaricus</i>	Serranidae	\$11.18 ± 0.7	531.9 ± 26.3	2.4%
<i>Epinephelus stoliczkae</i>	Serranidae	\$11.18 ± 0.7	296.2 ± 3.7	0.4%
<i>Anyperodon leucogrammicus</i>	Serranidae	\$11.18 ± 0.7	300.0 ± 0.0	0.2%
<i>Epinephelus areolatus</i>	Serranidae	\$11.18 ± 0.7	282.6 ± 3.4	10.6%
<i>Carangoides bajad</i>	Carangidae	\$12.06 ± 1.4 *	359.9 ± 8.0	3.5%
<i>Cetoscarus bicolor</i>	Scarinae, Labridae	\$14.40 ± 1.5 *	443.3 ± 14.0	0.5%
<i>Epinephelus summana</i>	Serranidae	\$14.58 ± 2.0 *	330.0 ± 8.0	1.6%
<i>Variola louti</i>	Serranidae	\$25.20 ± 1.4 *	443.3 ± 11.1	2.5%
<i>Plectropomus areolatus</i>	Serranidae	\$25.92 ± 2.5 *	378.8 ± 17.6	1.7%
<i>Plectropomus pessuliferus marisrubri</i>	Serranidae	\$26.43 ± 1.2 *	596.2 ± 28.3	1.3%
<i>Cheilinus undulatus</i>	Labridae	\$26.44 ± 3.5 *	783.3 ± 53.3	0.4%

*Plectropomus pessuliferus marisrubri* (“nagil”) and *C. undulatus* (Napoleon wrasse) garner the highest prices per kilogram in the market, worth \$26.43/kg and \$26.44/kg respectively (Table 3). The “nagil” is more abundant in the markets, averaging 13 individuals per visit, as opposed to an average of four individuals for the Napoleon wrasse. *Plectropomus areolatus* and *V. louti* are also highly valuable worth

\$25.92/kg and \$25.20/kg respectively. On average, there are 17 *P. areolatus* individuals at the fish market. *Variola louti* is more common, averaging 25 individuals per visit. *Plectropomus pessuliferus marisrubri*, *P. areolatus* and *V. louti* are the three most valuable grouper species at the fish market; most other grouper species all fall under the name “hammour” and are sold indiscriminately from each other for \$11.18/kg. *Carangoides bajad*, a jack, is a relatively valuable species, worth \$12.06 per kilo. It is typically found in the markets in relatively high abundances, but often in smaller sizes. Parrotfishes are also often found in high abundance at the fish market. Due to the similar appearances of many parrotfish, they are rarely separated by species. Most parrotfish are collectively referred to as “harid” and are priced \$10.38/kg. *Cetoscarus biocolor* is the only parrotfish with a species-specific price; they collect \$14.40/kg. That species is easily identifiable and often larger than most other parrotfish in this region. Many of the small fish, including small snappers, surgeonfishes, spadefishes, squirrelfishes and others, are sold indiscriminately from each other worth \$5.40/kg.

## DISCUSSION

### *4.1. Ecosystem Services in Saudi Arabia*

The provisioning service of coral reefs in the Red Sea appears to be stable after early stages of reef degradation due to coral bleaching. While our results indicate that the reef-based fisheries still hold their potential value despite benthic degradation, a shift from high-value carnivorous species to a dominance of lower-value herbivores was documented post-bleaching. There are likely significant changes to the fish community that have yet to become apparent in the Farasan Banks region associated with the loss of live coral cover. Declines in coral cover are often followed by increases in algal cover which in turn can support high herbivorous biomass. This can buffer the effects to the fisheries due to the maintenance or increase in overall biomass. However, even herbivorous species can eventually be impacted by the lack of structural complexity on reefs and dramatically affect fisheries revenues (Rogers et al. 2014, 2017). Other studies have emphasized that it can take many years following a bleaching event for the effects to fully be realized (Graham et al. 2007; Rogers et al. 2017). This study is not the end point for these reefs and these fish assemblages. As they continue to recover and/or degrade, ongoing monitoring is necessary to understanding how the provisioning of service in the Red Sea will be impacted.

#### *4.1.1. Reef Valuations*

Global and anthropogenic stressors result in numerous threats to the delivery of natural ecosystem services. As oceans warm and acidify, coral reefs become more

susceptible to bleaching and less able to recover. Eutrophication on reefs promotes algal growth which can outcompete coral recruits (Graham et al. 2015). These threats limit the ability for coral reefs to recover and therefore hinders their ability to provide their natural ecosystem services, including reef fish provisioning. We found a significant correlation between coral cover and total value of the reef, which may be an indication for what may happen to reef-based fisheries if habitat degradation continues.

Although we saw significant differences between the fish community composition of reefs sampled in 2014/15 compared to 2019, there was no significant difference between the potential revenues generated from those reefs. The average potential revenue per reef was slightly lower after the bleaching event, however the difference is not statistically significant. Both 2014/15 and 2019 reefs have a wide variety of potential revenues, ranging from under 2,000 USD/hectare to over 20,000 USD/hectare. It is important to note that the revenues calculated are potential revenues, not actual landing values. Much of the potential revenue from after the bleaching event is generated from less targeted herbivorous fishes. If the fishers switch to targeting the abundant herbivorous species, this provisioning service will likely remain stable in years immediately following bleaching events. However, this may imply a significant change to fishing practices, such as changes in gear and location; instead of using hook and line methods on reef edges, fishers will need to spend more time using traps and gillnets on the reef flats in order to catch higher numbers of

herbivores. Importantly, our estimates of how much revenue can be generated per reef are fisheries-independent; they are not reliant on landing data.

Many estimates of reef valuation solely employ fishery-dependent data, although that data often does not encompass the full reef community. This data includes species composition, effort estimates and price estimates, determined from landing site surveys and fisher interviews (Cesar et al. 2000; Grandcourt and Cesar 2003; Cruz-Trinidad et al. 2011). While these data are valuable, they do not represent the entire fish community, nor the entire potential revenue. One other study also utilized UVC to ascertain a change in the fish community following a disturbance, but the fisheries assessments were calculated using only fishery-dependent data (Cesar et al. 2000). The total potential revenue for a reef is likely to include non-target and less targeted fish species, therefore utilizing catch data alone is not an accurate representation. It is known that an increase in herbivorous fish following a bleaching event, may be what keeps the fisheries profitable, provided that the fishers catch those species (Cesar et al. 2000; Rogers et al. 2017). The only fishery that became more profitable in the Philippines following the 1998 mass bleaching event was the shallow water net fishery which targets grazing herbivores (Cesar et al. 2000). Similarly, in order for Saudi Arabian reefs to maintain their value, fishers will need to target parrotfish and other herbivorous species which became more abundant after the bleaching event. This requires a shift in fishing effort, more time using non-traditional fishing methods such as trapping and netting and less time using hook and line. In other areas of the world herbivores are caught using traps (Graham et al. 2007) or

spears (Bejarano Chavarro et al. 2014). The central coast of the Saudi Red Sea has been a hub of fishing for centuries (Gladstone 2002; Jeddah Facts and Figures 2017). Generation after generation has targeted the same species, in the same locations, using the same fishing methods (Gladstone 2002; Tesfamichael and Rossing 2012). The main advancement in technology occurred in the 1980s when most boats switched from wind power to gasoline engines (Tesfamichael and Rossing 2012). Increases in the number of fishers in recent decades led to largely overharvested waters. As the reefs here continue to change, fishers may need to deviate further from traditional fishing methods in order for the reef-based fisheries to remain sustainable and profitable.

#### *4.1.2. Non-Provisioning Ecosystem Services*

In accord with the Saudi Vision 2030, tourism is expected to drastically increase, which may markedly increase the ecosystem services value of coral reefs in the Saudi Red Sea (Frag 2019). In many other regions, the revenue generated from reef-based tourism is far higher than that generated by reef-based fisheries (Cruz-Trinidad et al. 2011; Gill et al. 2015). It is primarily due to the lack of international tourism in this region that fisheries are the most valuable service offered by Saudi reefs. Tourism, including recreational fishing, snorkeling, diving and boat trips, is expected to greatly increase with the development of the “mega city”, NEOM and other coastal development including The Red Sea Project. (Frag 2019). In 2019, Saudi Arabia began issuing tourist visas and began promoting the country as a tourist

destination. While tourism is currently minimal, it is expected to rapidly increase in the coming years. With these developments, both the benefits derived from coral reefs and the threats to coral reefs are expected to increase. Reef-based tourism can be highly profitable, more so than reef-based fisheries (Elliff and Kikuchi 2017; Spalding et al. 2017). Additionally, in these developed areas, marine protected areas are planned in an effort to protect local marine life. However, coastal development and tourism can severely damage natural ecosystems (Davenport and Davenport 2006; Mora 2008), limiting their delivery of natural ecosystem services. Development can destroy natural habitats, increase eutrophication and pollution and ecologically isolate populations (Mora 2008). As these acute anthropogenic stressors increase, coupled with global change impacts on Saudi Arabian coral reefs, careful monitoring and management is vital to keeping these ecosystems functioning properly.

#### ***4.2. Reef Degradation in Saudi Arabia***

Following the bleaching event in 2015/16, reefs in the central southern Red Sea are showing signs of degradation including decreased coral cover and increased algal cover. Because many of these reefs exhibit decreases in live coral cover but remain structurally complex, we believe that changes to the benthos in the Farasan Banks may still be underway. Accompanying the changes in the benthic community, there have been subsequent changes in the fisheries targeted fish community. As changes in benthic community are expected to continue, whether they begin to recover or continue to degrade, we also expect changes in the associated fish community.

#### *4.2.1. Benthic Cover*

The loss of symbiotic algae from which corals receive the majority of their energy is referred to as coral bleaching. Coral bleaching is a natural response to an external stressor. Only when the stressor persists for an extended period of time does colony death occur. Corals can survive for weeks to months bleached depending on the coral species and other environmental conditions. Unusually high temperatures in the Red Sea persisted from August-December 2015 (Monroe et al. 2018; Geneviev et al. 2019), causing mass coral mortality in some regions. That mortality was the first step in changing the benthic composition of reefs in the Farasan Banks.

As expected, there was a significant change in the benthic communities on these reefs after the mass coral bleaching event. The changes in benthic cover of these reefs were driven by the loss in coral cover. This loss in coral cover was accompanied by an increase in algal cover. The primary changes in benthic communities after the bleaching event were the loss of hard and soft corals. Higher levels of corals are generally considered indicative of healthy reefs compared to degraded ones. Furthermore, the reefs from after the bleaching event are associated with characteristics such as dead coral, rubble and algae, all of which are indicative of degrading reefs. Dead coral produces rubble and also creates bare substrate upon which algae can settle (Yadav et al. 2016). Algae often settles and grows faster than coral recruits, which is why bleaching events can lead to algal phase shifts (McCook et al. 2001; Otaño-Cruz et al. 2019). A wide range in coral cover measurements after the bleaching event indicate that the reefs are in various states of degradation and



recovery. Reefs surveyed before the bleaching event showed greater similarity than reefs surveyed after the bleaching event. This may be the result of variation in the impacts of the bleaching (due to e.g., disproportionate impacts among coral species or among reefs), or it may be due to variation in the recovery rates of coral communities post-bleaching, which is congruent with our findings that the reefs after the bleaching event have a wider variability in benthic state.

In addition to a shift in the benthic community, coral bleaching can lead to a change in the physical structure of coral reefs (Bozec et al. 2015). Although the link between declining coral cover and substrate rugosity has been well documented, (Alvarez-Filip et al. 2013; Leon et al. 2015; Spalding and Brown 2015), we do not yet see evidence of this coupling in the Red Sea. The bleaching event began about 3.5 years before the 2019 reef surveys were conducted. The breakdown of structure can take several years to decades following a bleaching event (Graham et al. 2007; Bozec et al. 2015). The breakdown can be expedited by the presence of bioeroders (Magel et al. 2019) or weather disturbances in the area. Due to the lack of storms in the Red Sea, it is likely that the structural complexity will take longer to break down after a bleaching event than in other tropical areas around the world. Even though coral cover has declined, the reefs are still structurally intact.

#### *4.2.2. Fish Community*

Coupled with a shift in the benthic communities on these reefs, we found a significant shift in the fisheries targeted fish communities as well. Congruent with the

increase in macroalgae, there was a 50% increase in herbivorous fish immediately following the bleaching event, in accord with other studies (Rogers et al. 2017; Robinson et al. 2019). Conversely, we saw a decrease in the number of carnivorous and omnivorous fish following the bleaching event. This result is in accord with other studies that have found declines in carnivores and omnivores after a bleaching event (Lindahl et al. 2001; Rogers et al. 2014); this likely occurs because the prey for those species was affected by the bleaching, resulting in repercussions ascending through the food web. Following bleaching events, the settlement and recruitment of small prey species is altered (Booth and Beretta 2002; McCormick et al. 2010), which can in turn affect higher level species, including serranids (Pratchett et al. 2008; Wen et al. 2013). In addition to these broad scale assemblage changes, a SIMPER analysis identified key species that had significant impacts on the overall differences between the two communities. The four species most responsible for the change in fish community were herbivores. All of those species exhibited two- or three-fold increases in biomass following the bleaching event. Additionally, those species all feed primarily on filamentous or leafy algae (Lieske and Myers 2004), characteristic of degrading reefs. Among the parrotfish species, *C. sordidus* is an excavator, and *S. niger* and *S. ferrugineus* are both scrapers (Bellwood and Choat 1990). Both excavators and scrapers have exhibited enhanced growth rates after a disturbance, with a peak two years following the disturbance (Taylor et al. 2019), congruent with an increase in algal cover after a disturbance. These SIMPER results are consistent with the overall result of increasing herbivorous fish biomass following the bleaching event

of 2015. A shift in trophic guilds from more carnivorous species to more herbivorous species was exhibited in both the overall change in biomass, and several species-specific size changes. The species that increased the most in biomass are largely from the Scarinae subfamily and Acanthuridae family, both of which feed on algae, a key feature of degraded reefs. The species with the greatest declines in biomass were carnivorous and omnivorous, congruent with other studies (Lindahl et al. 2001; Rogers et al. 2014, 2018). Herbivores *N. elegans* and *N. unicornis* exhibited larger mean sizes after the bleaching event than before. These herbivorous species likely benefited from the increase in algal cover after the bleaching event (Taylor et al. 2019). Additionally, *P. pessuliferus marisrubri* exhibited smaller mean sizes following the bleaching event, potentially caused by recruits and juveniles exhibiting decreased growth rates due to a lack of prey (Wen et al. 2013).

The changes we saw in the fish community are in accord with several other studies investigating direct (e.g. Luckhurst and Luckhurst 1978; Wismer, Hoey, and Bellwood 2009) and indirect (e.g. Wilson and Fisher 2008; Trebilco et al. 2015) effects of disturbances on fish communities. The species that directly rely on live coral, corallivores for example, will decline the most rapidly after a bleaching event (e.g., Yahya et al. 2011). Generally, those species that will be affected earliest by coral bleaching, are not target fisheries species; however, they may be the prey of target species. Species higher up the food chain can be affected by the declines in lower level species; it can take around one year for these changes to become apparent in the fish community (Booth and Beretta 2002). Adult individuals of large-bodied species,

targeted by fishers, are not likely to be significantly affected because they do not rely upon live coral. However, the settlement behavior of juvenile large-bodied species is likely to be affected (Feary et al. 2007; Bell et al. 2013; Nanami et al. 2013; Wen et al. 2013). Therefore, responses by these-fisheries relevant species to declining coral cover is likely more indicative of settlement preference or juvenile needs than adult preference (Feary et al. 2007). Fish will preferentially settle on live coral rather than dead coral or rubble (Yahya et al. 2011). The adults present when a bleaching event occurs will not be directly affected by the bleaching or loss in coral cover. However, they may be affected by a decrease in prey availability (Nanami et al. 2013). The larger issue is that these species may experience recruitment failure to degraded reefs. This implies that the changes to fisheries relevant species will not be apparent until years following the bleaching event.

The link between coral cover and fish biomass has been documented before (Wismer et al. 2009), as well as overall changes in community structure in relation to declining coral cover (e.g., Feary et al. 2007; Kuffner et al. 2007; Robinson et al. 2019). Importantly, we found significant correlations between coral cover and several fish community parameters. We found correlations between coral cover and overall biomass, in accord with several other studies (Wismer et al. 2009; Rogers et al. 2017). We also found a correlation between coral cover and species richness, as have several other studies (Wilson and Fisher 2008; Robinson et al. 2019). This result implies that as the coral cover continues to decrease on these reefs, so may the overall biomass and species richness among fish communities.

In addition to coral cover, physical complexity is an important measure of reef health often associated with fish community. Rugosity or physical complexity is a measure of how much structure extends away from the reef substrate. This complexity provides habitat and shelter for many species and mediates predator prey interactions (Harborne et al. 2012; Kerry and Bellwood 2012; Trebilco et al. 2015). Rugosity is found to affect many facets of the fish community, including species richness (Luckhurst and Luckhurst 1978; Graham et al. 2007; Kuffner et al. 2007; Walker et al. 2009), species diversity (Darling et al. 2017; Magel et al. 2019), abundance (Walker et al. 2009; Darling et al. 2017; Magel et al. 2019), and biomass (Friedlander et al. 2003; Harborne et al. 2012; Trebilco et al. 2015; Darling et al. 2017). Furthermore, decreases in coral cover, coupled with decreases in substrate rugosity, had far worse effects on the fish community than decreases in coral cover alone (Emslie et al. 2014). Many fish use coral for shelter and protection, which standing dead coral will still provide. Fish will utilize the structure provided by live, dead and bleached corals at similar rates. When the structure breaks down, there is a more significant decline in habitat use (Yahya et al. 2011). There are other links between benthic states, for example a strong negative correlation between complexity and algae (Graham and Nash 2013), both indicative of degrading reefs. Furthermore, coral cover is often linked with substrate complexity (Graham and Nash 2013; Emslie et al. 2014). We expected to see a link between coral cover and rugosity here in the Red Sea, however no such link was found. There is some evidence that degradation in reef structure may take years to decades following the bleaching event (Graham et al. 2007; Bozec et al. 2015), thus

there may be a link between coral cover and rugosity on these reefs in the coming years. Unfortunately, degrading reefs are less able to rebuild themselves than healthy ones; the rubble of dead coral shifts so much that coral recruits cannot settle upon it (Fox and Caldwell 2006). The loss of coral cover and complexity leads to a loss of key ecosystem function and services, notably fisheries productivity.

#### ***4.3. Fisheries in Saudi Arabia***

Despite changes in the overall fish communities, the reef-based fisheries appear to resistant to the early stages of reef degradation in the Farasan Banks. Reef-based fisheries are often able to withstand the early stages of reef degradation because the large bodied fishery species are generally less affected in the short term than smaller species (Cesar et al. 2000; Grandcourt and Cesar 2003; Rogers et al. 2017). However, this does not indicate that they are necessarily resilient to later stages of reef degradation. By one estimate, on reefs with little no live coral and no structural complexity, the only fish that will remain are small herbivores, which cannot sustain a reef-based fishery (Rogers et al. 2017). Compounding the issue of habitat degradation, it is likely that these Saudi Arabian reefs have been overfished for decades (Jin et al. 2012; Tesfamichael and Rossing 2012).

There is a large discrepancy between composition, abundance and size of species seen on the reefs compared to those seen in the markets. Large groupers dominate the fish market while they are rare in the surveys. Even before the bleaching event, large groupers were rare on Saudi Arabian reefs which may be an indication of

overfishing (Kattan et al. 2017). Groupers are the most abundant species by count and biomass in the markets and they are worth the most in revenue potential. In other regions of the world, groupers are also highly targeted by reef fishers (Rhodes and Tupper 2007; Bejarano Chavarro et al. 2014; Huliselan et al. 2017; Giglio et al. 2018). Following groupers, parrotfish are the next most valuable group. Parrotfish biomass increased on the reefs after the bleaching event. In other regions, when the grouper fishery is closed seasonally, fishers will more heavily target herbivorous fish (Bejarano Chavarro et al. 2014). A key issue is the discrepancy between what is seen on the reef and what is sold at the fish markets, from species composition to size and abundance. However, our surveys were conducted at a depth of 10m, there is potential that these grouper species are residing at deeper depths.

Saudi Arabian reef-based fisheries are threatened by habitat degradation and overfishing. Overexploitation and habitat degradation are the two major drivers of environmental change, responsible for local extinctions and loss of ecosystem services worldwide. The top down effect of overexploitation is coupled with the bottom up effects of habitat degradation (Wilson et al. 2008). Our results are congruent with other studies which have found that reef-based fisheries will be resilient during the initial phases of coral bleaching and reef degradation (Graham et al. 2007; Rogers et al. 2017; Robinson et al. 2019). While the fishery may be resilient to the initial stages of reef degradation, to withstand the issues of overfishing and further habitat degradation, fishers may need to devote more time to targeting the more abundant herbivorous fish, allowing the larger bodied carnivorous fish populations to recover.

The fishery could temporarily and sustainability start fishing those species while letting the stocks of grouper to rebound (Rogers et al. 2017). However, herbivorous fish play an important role in the recovery of coral reefs after disturbances by cropping algae and creating space where coral recruits may settle (Hughes et al. 2007) so targeting them needs to be done with the utmost caution.

There are many limitations to effective fisheries management, particularly in Saudi Arabia. The lack of compliance with fishing regulations is an issue prevalent in numerous tropical fisheries (PERSGA 2006; Bailey and Sumaila 2015; Katikiro and Mahenge 2016; Carvalho et al. 2019). In other areas, an issue is that there are numerous landing sites spread over great distances (Bailey and Sumaila 2015). In Saudi Arabia, fishers must stop at a coast guard station before and after each trip. Therefore, there are opportunities for fisheries enforcement during these stops. In the Farasan Banks, it is likely that fisheries are more heavily affected by overfishing than by the habitat degradation due to coral bleaching. However, both challenges can be mitigated with effective fisheries management. Shifts in benthic and fish community that were observed in this study provide evidence for potential long-term impacts which will require novel management approaches for reef based fisheries to remain viable in the future.



## CONCLUSIONS

The results of our reef valuations seem to indicate that the artisanal fishery in Saudi Arabia is resistant to the early stages of reef degradation due to coral bleaching, however, notable changes in the composition of the fish (i.e., an increase in herbivorous species and a decrease in carnivorous species) indicate that severe changes may be yet to come. An increase in herbivorous species coincided with an increase in macroalgal cover, a key feature of degrading reefs. Reefs are dynamic ecosystems that are constantly and often rapidly changing, from benthic state to fish community. Continued monitoring of the benthic state, including coral cover and rugosity measurements, as well as monitoring fish populations, is necessary to determine any long-term impacts from the 2015/16 bleaching event. Furthermore, there are currently few to no fishing regulations in this area. The fish community is vitally important to the recovery of these reefs, therefore implementing effective legislation is vital to the longevity of this fishery, be it marine protected areas, catch quotas or size limits. Effective fishing regulation can make the fish communities healthier which will enable them to recover from future disturbances.

## REFERENCES

- Albert JA, Olds AD, Albert S, Cruz-trinidad A (2015) Reaping the reef: Provisioning services from coral reefs in Solomon Islands. *Marine Policy* 62:244–251
- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports* 3:1–5
- Ampou EE, Johan O, Menkes CE, Niño F, Birol F, Ouillon S, Andrefouet S (2017) Coral mortality induced by the 2015-2016 El-Niño in Indonesia: The effect of rapid sea level fall. *Biogeosciences* 14:817–826
- Anderson AB, Batista MB, Gibran FZ, Félix-Hackradt FC, Hackradt CW, García-Charton JA, Floeter SR (2019) Habitat use of five key species of reef fish in rocky reef systems of southern Brazil: evidences of MPA effectiveness. *Marine Biodiversity* 49:1027–1036
- Arkema KK, Verutes G, Bernhardt JR, Clarke C, Rosado S, Canto M, Wood SA, Ruckelshaus M, Rosenthal A, McField M, De Zegher J (2014) Assessing habitat risk from human activities to inform coastal and marine spatial planning: A demonstration in Belize. *Environmental Research Letters* 9:
- Arkema KK, Verutes GM, Wood SA, Clarke-samuels C, Rosado S (2015) Embedding ecosystem services in coastal planning leads to better outcomes for people and nature. *PNAS*
- Bailey M, Sumaila UR (2015) Destructive fishing and fisheries enforcement in eastern Indonesia. *Marine Ecol* 530:195–211
- Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* 80:435–471
- Ban NC, Davies TE, Aguilera SE, Brooks C, Cox M, Epstein G, Evans LS, Maxwell SM, Nenadovic M (2017) Social and ecological effectiveness of large marine protected areas. *Global Environmental Change* 43:82–91
- Bejarano Chavarro S, Mumby PJ, Golbuu Y (2014) Changes in the spear fishery of herbivores associated with closed grouper season in Palau, Micronesia. *Animal Conservation* 17:133–143
- Bell JD, Ganachaud A, Gehrke PC, Griffiths SP, Hobday AJ, Hoegh-Guldberg O, Johnson JE, Le Borgne R, Lehodey P, Lough JM, Matear RJ, Pickering TD, Pratchett MS, Gupta A Sen, Senina I, Waycott M (2013) Mixed responses of tropical Pacific fisheries and aquaculture to climate change. *Nature Climate Change* 3:591–599
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* 28:189–214
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching

- event. *Marine Ecology Progress Series* 245:205–212
- Bozec YM, Alvarez-Filip L, Mumby PJ (2015) The dynamics of architectural complexity on coral reefs under climate change. *Global Change Biology* 21:223–235
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bulletin of Marine Science* 32:269–276
- Brock VE (1954) A Preliminary Report on a Method of Estimating Reef Fish Populations. *Journal of Wildlands Management* 18:297–308
- Bruckner AW, Dempsey AC (2015) The Status, Threats, and Resilience of Reef Building Corals of the Saudi Arabian Red Sea. *Springer Earth System Sciences*
- Bruno J, Siddon C, Witman J, Colin P, Toscano M (2001) El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* 20:127–136
- Burger J, Gochfeld M, Batang Z, Alikunhi N, Al-jahdali R, Al-jebreen D, Aziz MAM, Al-suwailem A (2014) Fish consumption behavior and rates in native and non-native people in Saudi Arabia. *Environmental Research* 133:141–148
- Carilli JE, Norris RD, Black B, Walsh SM, Mcfield M (2010) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biology* 16:1247–1257
- Carvalho S, Kürten B, Krokos G, Hoteit I, Ellis J (2019) The Red Sea. *World Seas: An Environmental Evaluation*. pp 49–74
- Cesar H, Pet-Soede L, Quibilan MCC, Aliño PM, Arceo HO, Bacudo I V, Fancisco H (2000) First Evaluations of the Impacts of the 1998 Coral Bleaching Event to Fisheries and Tourism in the Philippines. 41–58
- Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: Implications of transect width and species selection. *Marine Ecology Progress Series* 158:241–248
- Cheung WWL, Reygondeau G (2016) Large benefits to marine fisheries of meeting the 1.5°C global warming target. 354:1–5
- Coker DJ, Nowicki JP, Graham NAJ (2017) Influence of coral cover and structural complexity on the accuracy of visual surveys of coral-reef fish communities. *Journal of Fish Biology* 90:2425–2433
- Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries* 24:89–126
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9:286–307
- Costanza R, D’Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O’Neill R V, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world’s ecosystem services and natural capital. *Nature* 387:253–260
- Costanza R, de Groot R, Sutton P, Ploeg S Van Der, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. *Global Environmental Change* 26:152–158
- Costanza R, Mageau M (1999) What is a healthy ecosystem? *Aquatic Biology* 33:105–115

- Côté IM, Mosqueira I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis. *Journal of Fish Biology* 59:178–189
- Cruz-Trinidad A, Geronimo RC, Cabral RB, Aliño PM (2011) How much are the Bolinao-Anda coral reefs worth? *Ocean and Coastal Management* 54:696–705
- Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36:561–575
- Dasari HP, Langodan S, Viswanadhapalli Y, Vadlamudi BR, Papadopoulos VP, Hoteit I (2018) ENSO influence on the interannual variability of the Red Sea convergence zone and associated rainfall. *International Journal of Climatology* 38:761–775
- Davenport J, Davenport JL (2006) The impact of tourism and personal leisure transport on coastal environments: A review. *Estuarine, Coastal and Shelf Science* 67:280–292
- Dustan P, Doherty O, Pardede S (2013) Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. *PLoS ONE* 8:1–10
- Elliff CI, Kikuchi RKP (2017) Ecosystem services provided by coral reefs in a Southwestern Atlantic Archipelago. *Ocean and Coastal Management* 136:49–55
- Emslie MJ, Cheal AJ, Johns KA (2014) Retention of Habitat Complexity Minimizes Disassembly of Reef Fish Communities following Disturbance : A Large-Scale Natural Experiment. *PLoS ONE* 9:
- Facon M, Pinault M, Obura D, Pioch S, Pothin K, Bigot L, Garnier R, Quod JP (2016) A comparative study of the accuracy and effectiveness of Line and Point Intercept Transect methods for coral reef monitoring in the southwestern Indian Ocean islands. *Ecological Indicators* 60:1045–1055
- Farag AA (2019) The Story of NEOM City: Opportunities and Challenges. In: Attia S., Shafik Z., Ibrahim A. (eds) *New Cities and Community Extensions in Egypt and the Middle East*. Springer International Publishing, Cham, Switzerland, pp 35–50
- Feary DA, Almany GR, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153:727–737
- Ferrari R, Bryson M, Bridge T, Hustache J, Williams SB, Byrne M, Figueira W (2016) Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global Change Biology* 22:1965–1975
- Fox HE, Caldwell RL (2006) Recovery from blast fishing on coral reefs: a tale of two scales. *Ecological applications* 16:1631–1635
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253–264

- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224:1–30
- Froese R, Pauly D (2014) Fishbase.
- Fuad MAZ (2010) Coral Reef Rugosity and Coral Biodiversity. Department of Natural Resources, ITC
- Genevier LGC, Jamil T, Raitsos DE, Krokos G, Hoteit I (2019) Marine heatwaves reveal coral reef zones susceptible to bleaching in the Red Sea. *Global Change Biology* 25:2338–2351
- Giglio VJ, Ternes MLF, Luiz OJ, Zapelini C, Freitas MO (2018) Human consumption and popular knowledge on the conservation status of groupers and sharks caught by small-scale fisheries on Abrolhos Bank, SW Atlantic. *Marine Policy* 89:142–146
- Gill DA, Schuhmann PW, Oxenford HA (2015) Recreational diver preferences for reef fish attributes: Economic implications of future change. *Ecological Economics* 111:48–57
- Gladstone W (2002) Fisheries of the Farasan Islands (Red Sea). Naga, WorldFish Center Quarterly 25:30–34
- Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982/1983 event. *Bulletin of Marine Science* 69:79–109
- Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97
- Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *PNAS* 103:8425–8429
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* 21:1291–1300
- Grandcourt EM, Cesar HSJ (2003) The bio-economic impact of mass coral mortality on the coastal reef fisheries of the Seychelles. *Fisheries Research* 60:539–550
- de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, Hussain S, Kumar P, Mcvittie A, Portela R, Rodriguez LC, ten Brink P, Beukering P Van (2012) Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* 1:50–61
- Harborne AR, Mumby PJ, Ferrari R (2012) The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes* 94:431–442
- Harriott VJ (1999) Coral growth in subtropical eastern Australia. *Coral Reefs* 18:281–291

- Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World's Marine Ecosystems. *Science* 328:1523–1528
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83
- Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs JPA, Hoogenboom MO, Kennedy E V., Kuo CY, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373–377
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology* 17:360–365
- Huliselan N V., Wawo M, Tuapattinaja MA, Sahetapy D (2017) Present status of grouper fisheries at waters of Kotania Bay, Western Seram District Maluku Province. 89:
- Jin DI, Kite-Powell H, Hoagland P, Solow A (2012) A Bioeconomic Analysis of Traditional Fisheries in the Red Sea. *Marine Resource Economics* 27:137–148
- Katikiro RE, Mahenge JJ (2016) Fishers' Perceptions of the Recurrence of Dynamite-Fishing Practices on the Coast of Tanzania. *Frontiers in Marine Science* 3:1–14
- Kattan A, Coker DJ, Berumen ML (2017) Reef fish communities in the central Red Sea show evidence of asymmetrical fishing pressure. *Marine Biodiversity* 47:1227–1238
- Kerry JT, Bellwood DR (2012) The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs* 31:415–424
- Khan AQ, Aldosari F, Hussain SM (2016) Fish consumption behavior and fish farming attitude in Kingdom of Saudi Arabia ( KSA ). *Journal of the Saudi Society of Agricultural Sciences*
- Knudby A, LeDrew E (2007) Measuring Structural Complexity on Coral Reefs. *Proceedings of the American Academy of Underwater Sciences 26th Symposium* 181–188
- Kuffner IB, Brock JC, Grober-Dunsmore R, Bonito VE, Hickey TD, Wright CW (2007) Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environmental Biology of Fishes* 78:71–82
- Leon JX, Roelfsema CM, Saunders MI, Phinn SR (2015) Measuring coral reef terrain

- roughness using “Structure-from-Motion” close-range photogrammetry. *Geomorphology* 242:21–28
- Lieske E, Myers RF (2004) *Coral Reef Guide Red Sea*. HarperCollins Publishes Ltd, London
- Lindahl U, Öhman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin* 42:127–131
- Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013) Current Status and Future Prospects for the Assessment of Marine and Coastal Ecosystem Services : A Systematic Review. 8:
- Lough JM, Cantin NE (2014) Perspectives on massive coral growth rates in a changing ocean. *Biological Bulletin* 226:187–202
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49:317–323
- Magel JMT, Burns JHR, Gates RD, Baum JK (2019) Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Scientific Reports* 9:1–12
- Mapstone BD, Ayling AM (1998) An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. Great Barrier Reef Marine Park Authority
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: Interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380–391
- McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* 19:400–417
- McCormick MI (1994) Comparison of field methods for measuring surface tomography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* 112:87–96
- McCormick MI, Moore JAY, Munday PL (2010) Influence of habitat degradation on fish replenishment. *Coral Reefs* 29:537–546
- Monroe AA, Ziegler M, Roik A, Röthig T, Hardenstine RS, Emms MA, Jensen T, Voolstra CR, Berumen ML (2018) In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. *PLoS ONE* 13:1–13
- Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society Biological Sciences* 275:767–773
- Moradi-Lakeh M, Bcheraoui C El, Afshin A, Daoud F, Almazroa MA, Saeedi M Al, Basulaiman M, Memish ZA, Rabeeah AA Al, Mokdad AH (2016) Diet in Saudi Arabia : fi ndings from a nationally representative survey. *Public Health Nutrition* 20:1075–1081
- Morgan KM, Kench PS (2012) Skeletal extension and calcification of reef-building corals in the central Indian Ocean. *Marine Environmental Research* 81:78–82
- Myers, Ransom A., Worm, Boris (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283

- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1851
- Nanami A, Sato T, Takebe T, Teruya K, Soyano K (2013) Microhabitat association in white-streaked grouper *Epinephelus ongus*: Importance of *Acropora* spp. *Marine Biology* 160:1511–1517
- Ngoc QTK (2018) Assessing the value of coral reefs in the face of climate change: The evidence from Nha Trang Bay, Vietnam. 1:1–15
- Otaño-Cruz A, Montañez-Acuña AA, García-Rodríguez NM, Díaz-Morales DM, Benson E, Cuevas E, Ortiz-Zayas J, Hernández-Delgado EA (2019) Caribbean near-shore coral reef benthic community response to changes on sedimentation dynamics and environmental conditions. *Frontiers in Marine Science* 6:1–19
- PERSGA (2006) State of the Marine Environment, Report for the Red Sea and Gulf of Aden.
- Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Current Opinion in Environmental Sustainability* 7:37–43
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes-ecological and economic consequences.
- Rhodes KL, Tupper MH (2007) A preliminary market-based analysis of the Pohnpei, Micronesia, grouper (Serranidae: Epinephelinae) fishery reveals unsustainable fishing practices. *Coral Reefs* 26:335–344
- Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* 1:65–91
- Robinson JPW, Wilson SK, Jennings S, Graham NAJ (2019) Thermal stress induces persistently altered coral reef fish assemblages. *Global Change Biology* 25:2739–2750
- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* 24:1000–1005
- Rogers A, Blanchard JL, Mumby PJ (2017) Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology* 55:1041–1049
- Rowlands G, Purkis S, Bruckner A (2014) Diversity in the geomorphology of shallow-water carbonate depositional systems in the Saudi Arabian Red Sea. *Geomorphology* 222:3–13
- Ruttenberg BI, Hamilton SL, Walsh SM, Donovan MK, Friedlander A, DeMartini E, Sala E, Sandin SA (2011) Predator-induced demographic shifts in coral reef fish assemblages. *PLoS ONE* 6:
- Sale PF, Douglas A (1981) Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. *Environmental Biology of Fishes* 6:333–339
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*



3:

- Schmitt EF, Sluka RD, Sullivan-Sealey KM (2002) Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. *Coral Reefs* 21:216–223
- Shedrawi G, Harvey ES, McLean DL, Prince J, Bellchambers LM, Newman SJ (2014) Evaluation of the effect of closed areas on a unique and shallow water coral reef fish assemblage reveals complex responses. *Coral Reefs* 33:579–591
- Sil Â, Rodrigues AP, Carvalho-Santos C, Nunes JP, Honrado J, Alonso J, Marta-Pedroso C, Azevedo JC (2016) Trade-offs and synergies between provisioning and regulating ecosystem services in a mountain area in Portugal affected by landscape change. *Mountain Research and Development* 36:452–464
- Spaet JLY, Berumen ML (2015) Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea. *Fisheries Research* 161:356–364
- Spalding M, Burke L, Wood SA, Ashpole J, Hutchison J, zu Ermgassen P (2017) Mapping the global value and distribution of coral reef tourism. *Marine Policy* 82:104–113
- Spalding MD, Brown BE (2015) Warm-water coral reefs and climate change. *Science* 350:769–771
- Sully S, Burkepille DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. *Nature Communications* 10:1–5
- Taylor BM, Benkwitt CE, Choat H, Clements KD, Graham NAJ, Meekan MG (2019) Synchronous biological feedbacks in parrotfishes associated with pantropical coral bleaching. *Global Change Biology* 1285–1294
- Tesfamichael D, Pauly D (2015) The Red Sea Ecosystem and Fisheries. *Coral Reefs of the World*. Springer, pp 203
- Tesfamichael D, Rossing P (2012) Reconstructing Red Sea Fisheries Catches of Saudi Arabia: National Wealth and Fisheries Transformation. *Fisheries Centre Research Reports* 20:153–178
- Townsend M, Davies K, Hanley N, Hewitt JE, Lundquist CJ, Lohrer AM (2018) The challenge of implementing the marine ecosystem service concept. *Frontiers in Marine Science* 5:1–13
- Trebilco R, Dulvy NK, Stewart H, Salomon AK (2015) The role of habitat complexity in shaping the size structure of a temperate reef fish community. *Marine Ecology Progress Series* 532:197–211
- Tsikliras AC, Polymeros K (2014) Fish market prices drive overfishing of the ‘big ones.’ *PeerJ* 1–9
- Walker BK, Jordan LKB, Spieler RE (2009) Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. *Journal of Coastal Research* 10053:39–48
- Weijerman M, Gove JM, Williams ID, Walsh WJ, Minton D, Polovina JJ (2018) Evaluating management strategies to optimise coral reef ecosystem services. *Journal of Applied Ecology* 55:1823–1833

- Wen CKC, Pratchett MS, Almany GR, Jones GP (2013) Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. *Coral Reefs* 32:389–398
- Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski B, Craig P, McIlwain JL, Brainard RE (2011) Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western pacific. *Journal of Marine Biology*
- Wilson SK, Fisher R, Pratchett M, Graham N, Dulvy N, Turner R, Cakacaka A, Polunin N, Rushton S (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology* 14:2796–2809
- Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: Relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* 376:45–54
- Yadav S, Rathod P, Alcoverro T, Arthur R (2016) “Choice” and destiny: the substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. *Coral Reefs* 35:211–222
- Yahya SAS, Gullström M, Öhman MC, Jiddawi NS, Andersson MH, Mgaya YD, Lindahl U (2011) Coral bleaching and habitat effects on colonisation of reef fish assemblages: An experimental study. *Estuarine, Coastal and Shelf Science* 94:16–23
- Young GC, Dey S, Rogers AD, Exton D (2018) Correction: Cost and time-effective method for multi-scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models (*PLoS ONE* (2018)12: 4 (e0175341) DOI : 10.1371/journal.pone.0175341). *PLoS ONE* 12:1–18
- Aichi Biodiversity Targets. [www.cbd.int/sp/targets/](http://www.cbd.int/sp/targets/)
- (2006) Statistical Indications About Fisheries in the Kingdom of Saudi Arabia.
- (2017) Jeddah Facts and Figures: Jeddah Annual Report 2016-2017.

## APPENDIX

Appendix Table 1. The results of the PERMANOVA confirming that shelf position cannot explain the changes in the fish community in 2019 ( $p=0.08$ ). “Shelf position” is a categorical variable (inshore, midshelf, offshore). “Fisheries” refers to the biomass of fisheries relevant species from the reef surveys.

	Df	Sum of Sq	Mean Sqs	F Model	R2	Pr(>F)
Fisheries\$shelf	2	1.165	0.58234	1.6372	0.00427	0.08
Residuals	763	271.397	0.35570		0.99573	
Total	765	272.561			1.00000	