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Fish diversity and distribution in the seagrass-coral reef continuum at two sites off the western coast of Isla Bastimentos, Bocas del Toro, Panama

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Abstract

Coral reefs are the most diverse marine ecosystem and the largest biogenic structure on Earth. They serve as shelter for many reef fishes and are a food source for resident and visiting fish species. In the tropics, coral reefs are often in close proximity to seagrass beds and the two contiguous marine habitats are not only highly interconnected but also highly understudied. The seagrass-coral reef continuum offers a wide array of services to human society as well as to various life stages of reef fishes resulting in diel, temporal, or yearly migrations of fish between the two habitats. Tropical reef fish diversity, abundance, and evenness were measured in both habitats in the morning and afternoon to determine if any significant differences in results between habitats or times of day could be observed. Underwater video recordings were taken of 15 m transects in the seagrass bed and coral reef at two sites, one sheltered and one more exposed, off Isla Bastimentos, Bocas del Toro, Panama. The recordings were used in calculating fish diversity, abundance, and evenness and in surveying the benthic composition of the coral reef. Sixteen transects were recorded in each habitat at each time of day at each site and a total of 3587 fish were observed representing 14 different families and 32 different species. Site 1 had low live coral coverage and was composed of mainly hard open substrate while Site 2 was composed mainly of macroalgae and live coral. Ultimately, no significant differences were found between fish abundance or evenness however, significant differences were found in fish diversity between the seagrass bed and coral reef ($P<0.001$, df=3493) as well as between the morning and the afternoon ($P<0.001$, df=3454). Based on these results, it can be concluded that habitat and time of day play significant roles in fish diversity and even though fish abundance and evenness were not significantly different, they generally aligned with conclusions made in previous studies.

Acknowledgements

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Introduction

Coral reefs

Coral reefs make up less than one percent of the Earth's surface and yet contain roughly twenty-five percent of all marine organism species. This makes them the most biodiverse marine ecosystem as well as the largest biogenic structure in the world (Mumby & Steneck 2008; Ahmadia et al. 2012). Corals are sessile marine invertebrates of the phylum Cnidaria and class Anthozoa that live in large colonies composed of identical individual polyps that act as a single organism. Polyps are tiny sac-like animals that have tentacles surrounding a main body cavity. They are highly dependent on the water column, from which they are able to obtain some food and into which some species release their gametes to be fertilized. Corals are separated into two types, soft corals and hard corals. Coral reefs form as polyps of hard corals secrete calcium carbonate which builds up over time to form a hard-exterior skeleton. Calcium carbonate is constantly being added to the skeleton which becomes the framework of the reefs and can result in reefs of varying architectural complexities (Sheppard et al. 2009).

The structural and topographical complexity of corals attribute to the diversity and abundance of the many marine organisms, especially fish which are associated with and utilize the coral for a variety of purposes (Grober-Dunsmore et al. 2007; Schrandt and Lema 2011; Graham and Nash 2013). Coral reefs provide shelter and habitats, along with various microhabitats, to a wide array of fishes. They also provide nutrients and foster an incredibly productive environment for primary producers such as zooplankton, algae, bacteria, and marine plants. This in turn creates a vast, complicated food web with echinoderms and coral reef fishes being main primary consumers (Graham et al. 2017). Due to the abundance of primary consumers, secondary consumers are also well supported in the coral reef ecosystem. This includes many other species of fish that inhabit or frequently visit reefs such as barracudas, sharks, and large seabasses. This diversity is all possible because of the coral reefs themselves which are very efficient at obtaining and recycling nutrients. The more complex corals are, the better they are at doing so. Additionally, the more complex the corals are, the more spaces are available to provide refuge to more fish and the more niches are provided for various fish species which decreases interspecies competition (Almany 2004; Johnson 2007).

While the tri-dimensionality of corals is important to marine biodiversity, it is also important in combination with their location along the continental coasts because they serve as major natural shoreline protectors. Coral reefs act as buffer zones that absorb the majority of wave and tropical storm impacts, lessening the force of the ocean when it reaches the shores of natural and manmade communities. This is beneficial as it decreases or eliminates many damaging effects that could occur to coastal habitats and coastal human societies around the world as a result of taking on water. Coral reefs protect the coasts from flooding, erosion, and they also provide a host of ecosystem services (Mumby & Steneck 2008). Some of the services provided are that of a local and global food resource, the potential to aid in scientific advances in drug development, the support of local economies, and the important part they play in many coastal cultural activities and practices (Mumby & Steneck 2008).

While some coral reefs are found in deeper waters, most occur in shallower tropical and subtropical waters between 30°N and 30°S. Coral reefs and seagrass beds are often found in close proximity in the tropics and coral reef fish biomass is usually greater when adjacent to seagrass beds (Heck 2008).

Seagrasses

Seagrasses are flowering plants of the order Alismatales. They are the only marine angiosperm and grow mainly in shallow marine environments (Orth et al. 2006). They are most commonly found along tropical and subtropical coastlines around the world, although they can also be found up through the Arctic. Seagrass is comprised of the above ground leaves that obtain energy through photosynthesis, the below ground horizontal rhizomes which secure the plant to the sediment, and the roots that extend further down from the rhizome into the ground to absorb more nutrients. They grow in varying size clusters ranging from small beds to vast meadows. Seagrass beds are extremely productive environments that also trap sediment, stabilize the ocean floor, and prevent soil erosion (Orth et al. 2006; Heck Jr. et al 2008). Seagrass ecosystems are a keystone environment for aquatic animals and provide food and shelter to many organisms (Connolly and Hindell 2006; Orth et al. 2006).

Seagrass meadows are both permanent, transient, and nursery habitats for a variety of fish species (Gullström et al. 2008; Espino et al. 2015). Many factors influence the abundance of tropical fish in seagrass beds such as canopy height, water depth, and distance to adjacent coral reef and mangrove environments (Dorenbosch et al. 2005; Gullström et al. 2008). Seagrass structural complexity appears to be important towards fishes and play a part in the trade-off between predation risk and food availability. Denser seagrass beds with higher canopies produce more coverage for smaller fishes to hide under in order to escape predation, but these conditions in turn also mean that there are more small fish which predators can consume. However, it is debated among scientist to what extent seagrass complexity and density actually contribute to fish population densities (Gullström et al. 2008).

The presence of fishes in seagrass fluctuates over time and is based on the specific fish species' life cycles, behavior, and seagrass area coverage (Espino et al. 2015). Many species migrate out of the seagrass to the coral reefs, but they do so at different rates. Other species migrate into the seagrass from surrounding coral reef and mangrove habitats daily in order to feed. Diel variation in fish densities in seagrass beds have been observed in temperate zones (Robertson 1980; Ryan 1981) although tropical fish densities are poorly documented (Robblee and Zieman 1984). Seagrass beds that are in closer proximity to coral reefs allow for these daily or yearly migrations to occur more conveniently.

Relationships between coral reef and seagrass habitats

Many fish interactions occur between seagrass and coral reef habitats, but the interlinkages between the two are not well studied nor understood (Dorenbosch et al. 2005; Unsworth et al. 2008). Non-coral habitats play an important role in the speciation and persistence of Caribbean fish taxa because, unlike in the Indo-Pacific, no species of Caribbean reef fish live and feed exclusively on corals (Paddack et al. 2009). Both seagrass and coral reef habitats play major roles in the life cycles of many tropical fish as ontogenetic niche shifts are very common (Honda et al. 2013; Kimirei et al. 2013). Some fish that live in coral reefs migrate to seagrass beds to mate or to lay their eggs and then return to the reefs. Many reef fish species use the seagrass beds as nurseries due to the different suitabilities of the coral reef and seagrass habitats for various life stages of fish. The two-dimensionality of the seagrass is more ideal for juvenile fish or smaller adult fish that are able to use the canopies for cover as well as for larger fish that either do not need to worry as much about predators or are the predators themselves. Medium sized fish are not as common in the seagrass beds and either tend to swim in larger agglomerations in the seagrass or stay in the tri-dimensional corals that provide more cover (Ogden and Zieman, 1977). By shifting between the two habitats, fish are able to exploit the benefits of each to their specific needs (Dorenbosch et al. 2007). Shifts between the two habitats are common around the world but happen more frequently in the Caribbean because of the specific habitat configuration such that coral reefs and seagrass are often in such close proximity and biomass and energy flow between the two are constant (Dorenbosch et al. 2007; Kimirei, et al. 2013).

Besides ontogenetic niche shifts by fish between the two habitats, some fish also migrate daily between habitats in order to feed in the seagrass beds and retreat back to the corals for shelter. Seagrass provides organic matter and living plant and epiphyte biomass that herbivorous reef fishes eat (Heck Jr. et al. 2008). In earlier studies (Goldman and Talbot 1976; Polunin 1996) of reef fishes it was found that most were carnivorous and had a biomass is 3-4 times that of herbivores which suggest that they must go elsewhere, for example to adjacent seagrass beds, to feed on larger primary consumers. Other studies regarding trophic connectivity have been done in the Western Atlantic as well as in other areas and have found similar trends which suggest that the migration of fish from corals reefs to seagrass is a general phenomenon (Heck Jr. et al. 2008). Due to the connectivity of fish communities between the two habitats, they often influence one another and any effects or stresses on one can have consequences on the other. However, connectivity between habitats is being altered and in some cases are diminishing due to anthropogenic effects (Heck et al. 2008).

Many fish species visit and can be found in both habitats. However, as the distance between habitats increase, similarity between fish assemblages in the two habitats is expected to decrease (Dorenbosch et al. 2007). This is likely due to the fact that environmental heterogeneity leads to variation in habitat quality which fosters more varied distribution of species and behavioral variation (Schrandt and Lema 2011; Schrandt et al. 2012). As the two habitats get further away from each other and become more geographically isolated, they become more homogenous and fish species tend not to overlap as much as fish need to face different physical and local challenges (Schrandt et al. 2012). The distance between habitats and the various environmental factors between as well as within habits influence fish diversity, abundance, evenness, and behavior (Gratwicke and Speight 2005).

Diel effects on coral reef fishes

The activity during various times of day differs between many reef fish species, both diurnal (day active fishes) and nocturnal (night active fishes), and leads to diel variations in the diversity and abundance of reef fish in both seagrass and coral reef habitats (Hobson 1975; Nagelkerken et al. 2000; Hitt et al. 2011). Feeding occurs during the active period of either type of fish and shelter finding occurs during the inactive period. The time during sunrise and sunset are transition phases for diurnal and nocturnal fishes and leave them most susceptible to predators. Hobson (1972) recognized three main periods within the transitions: coverage seeking of active fishes, an interim period, and emergence of inactive fishes. During this transition interval, fish diversity and activity increases in the water column with migrations occurring within the reef as well as migrations into and out of the reef. Light levels and visibility in the water due to the moon or the sun affect the rates at which fish transition, but it is hard to determine exactly when these transitions take place because the amount of light present is susceptible to frequent changes due to other factors such as cloud coverage and moon cycles (Hobson 1972).

Daily biotic factors, such as predator-prey relations and competition, and abiotic factors, such as temperature and tidal changes, are shown to affect fish behavior and abundance of reef fishes (Robblee and Zieman 1984). Routine movements appear to optimize fish survival by maximizing growth rate and minimizing predation risk (Hobson 1972; Hitt et al. 2011). Some noted categories of movements of reef fishes include migration between offshore feeding grounds and the shelter providing reef, migration within the reef from one location to another, and vertical migration in the water column above the reef (Hobson 1972). The benthic seascape seems to be a key factor in the daily routines and foraging movements of fish species between corals and seagrass in the Caribbean but is understudied (Hitt et al. 2011).

Location

Panama is a narrow Central American country with Costa Rica to the west and Colombia to the east. The isthmus of Panama formed roughly 2.8 million years ago and is a physical barrier that separates the Caribbean Sea of the Atlantic Ocean, which is situated along the northern coast of Panama, and the Pacific Ocean, which is situated on the southern coast. Panama is located in the tropics which means it has characteristically uniform temperatures year around and very little seasonal variation. The two distinct seasons are the dry season which lasts from January to March and the wet season which lasts from April to December.

The Bocas del Toro archipelago is located on the northwest coast of Panama in the tropical Western Atlantic Ocean. The area receives an annual rainfall of 3-5 m and intense rains and a lack of pronounced seasonal pattern, typical of Panama's Pacific coast, are characteristic of the area (Collin 2005; Dominici-Arosemana and Wolff 2005). The waves and current have a strong impact on the outer regions of the archipelago, while semi-lagoonal areas within the archipelago are more sheltered from waves due to the barrier created by some of the islands. This leads to varying communities of fish and other organisms throughout the archipelago. Fish species richness increases from sheltered to exposed areas and from low-complexity to intermediate and high-complexity zones. Fish species richness in Bocas del Toro is also related to substrate complexity. Exposed zones in Bocas del Toro are generally more physically complex and more diverse and abundant food resources are present in these zones. Algae and sessile invertebrates such, as sponges, increase the diversity of the substrate and foster increased diversity of fish. (Dominici-Arosemena and Wolff 2005).

The network of islands and reefs that make up the archipelago have some of the highest diversities and abundance of corals in shallow water (Dominici-Arosemena and Wolff 2005). This abundance of coral fosters a large diversity of marine organisms; however, diversity has started to decrease with global climate change, coral bleaching, and increased tourism of the islands (Munday et al. 2008) with the highest populated centers located on Isla Bastimentos, Isla Colón, and Isla Carenero (Dominici-Arosemena and Wolff 2005). The natural environment within the islands is starting to degrade with unsustainable tourism (Claiborne 2010) and overfishing of large predatory fish species (Windevoxhel and ter Heeedge 2008). With the environmental changes and anthropogenic effects, it is important to focus on the Bocas del Toro islands as they are home to over 100 species of fish that live in the coral reefs and in the other surrounding mangroves and seagrasses ecosystems (Dominici-Arosemana and Wolff 2005). Gobiidae, Pomacentridae, and Labridae are generally the most abundant functional groups in the region with species of Scaridae and Pomacentridae being the most common fish in sheltered zones (Dominici-Arosemana and Wolff 2005). Typically, there are large areas of seagrass beds right off of the reef that also surround many of the islands in the archipelago. *Thalassia testudinum* is the most abundant species of seagrass, out of the four species that are present in Panama, found in the seagrass beds in the area (Collin 2005).

The Bocas del Toro archipelago also contains Panama's first national marine park, Isla Bastimentos National Marine Park (*Parque Nacional Marino Isla Bastimentos* PNMIB) located on and around Isla Bastimentos. This Marine Protected Area (MPA), like others, is an "[area] designated for special protection to enhance the management of marine resources" (National Research Council 2001). PNMIB covers an area of 13,360 hectares of which 11,730 ha are marine (Guerrón-Montero, 2005). The park includes a wide array of terrestrial and marine ecosystems, including coral reefs, mangrove stands, and seagrass beds (Guerrón-Montero, 2005). The park's main goal is to conserve a broad range of ecosystems present in the region and the inclusion of all three distinct marine ecosystems gives it the potential to do so more effectively due to the connectivity of the ecosystems.

Previous research and knowledge gaps

Numerous studies have been conducted focusing on a single marine ecosystem, while little research has been done comparing multiple contiguous marine habitats. Many fish interactions that occur between seagrass and coral reef habitats and the degree to which fish communities are linked are still unknown (Dorenbosch et al. 2005). Some studies regarding connectivity between the continuous seagrass-coral reef gradients have been conducted (Dorenbosch et al. 2005) while others have been carried out examining the links between seagrass and coral reef habitats with over a hundred meters of separation in between. Incorporating more aspects and details such as benthic composition, multiple times of day, multiples seasons, etc. regarding each habitat result in a more comprehensive understanding of connectivity and behavioral patterns. Studies focusing on these gradients contribute to scientific understanding of the habitats themselves, the fish species that are present, biotic, and abiotic factors. Spending more time in each habitat also allows for the potential to discover new species being that more than 90% of the ocean is still undiscovered or undescribed (Mora et al. 2011). Only continued interest and efforts can aid in adding to the current understanding of the ocean and all of the organisms that live in it.

This study will examine how fish species diversity, abundance, and evenness differ at different times of day in the coral reef and contiguous seagrass bed off of Isla Bastimentos in the Caribbean Sea. The primary hypotheses of the study regarding fish diversity, abundance, and evenness between habitats at different times of day include: (1) If species richness increases from more sheltered to more exposed area, then Site 1 will have a higher richness than Site 2. (2) The morning data collection period should yield a higher total diversity of fish at each site since it is closer to the transition period of diurnal and nocturnal fish species. (3) The coral reefs should yield higher diversity of fish than the seagrass because they are more heterogeneous and structurally complex.

Research Question

Do reef fish species diversity, abundance, and evenness differ at varying times of day in the coral reef and adjacent seagrass bed at two sites off the western coast of Isla Bastimentos, Bocas del Toro, Panama?

Research Objectives

- To understand how fish populations differ based on time of day in two adjacent tropical habitats (coral reef and seagrass bed) on the Caribbean side of Panama.

Methods

Study area

This study was conducted at two sites off of the island of Bastimentos in the Bocas del Toro province of Panama. Sites were selected based on the presence of a coral reef and an adjacent seagrass bed as well as on the convenience of access by kayak (Figure 1). Site 1 (9°20'28"N, 82°12'32"W) is located on the western side of Isla Bastimentos just a little over 0.5 km from the main town of Old Bank and the main docks by kayak. Although not immediately situated next to any docks or houses, the site is in close proximity (approx. 200 m) to docks, is exposed, and experienced high boat traffic as boats came from and went to neighboring islands and popular snorkeling destinations. The seagrass bed and coral reef at the site are located approximately one to two hundred meters from the rocky cliffside of the island and also experienced some mild wave action. Site 2 (9°20'14"N, 82°11'57"W) is also located on the western side of Isla Bastimentos and is more secluded and sheltered from boat traffic, waves, and strong currents. Site 2 is located a little over 1.5 km from Old Bank by kayak. It is about 0.5 km from a settlement of a dozen houses and less than one hundred meters from an abandoned dock. Unlike Site 1, the seagrass and coral reef at Site 2 were both contiguous with mangroves. Once at the sites, the kayak was anchored to either dead coral, a large rock, or to mangrove roots. The locations where the transects were set up were selected randomly by swimming from the kayak to the closest area containing an expanse of seagrass or coral (Shen, 2016).

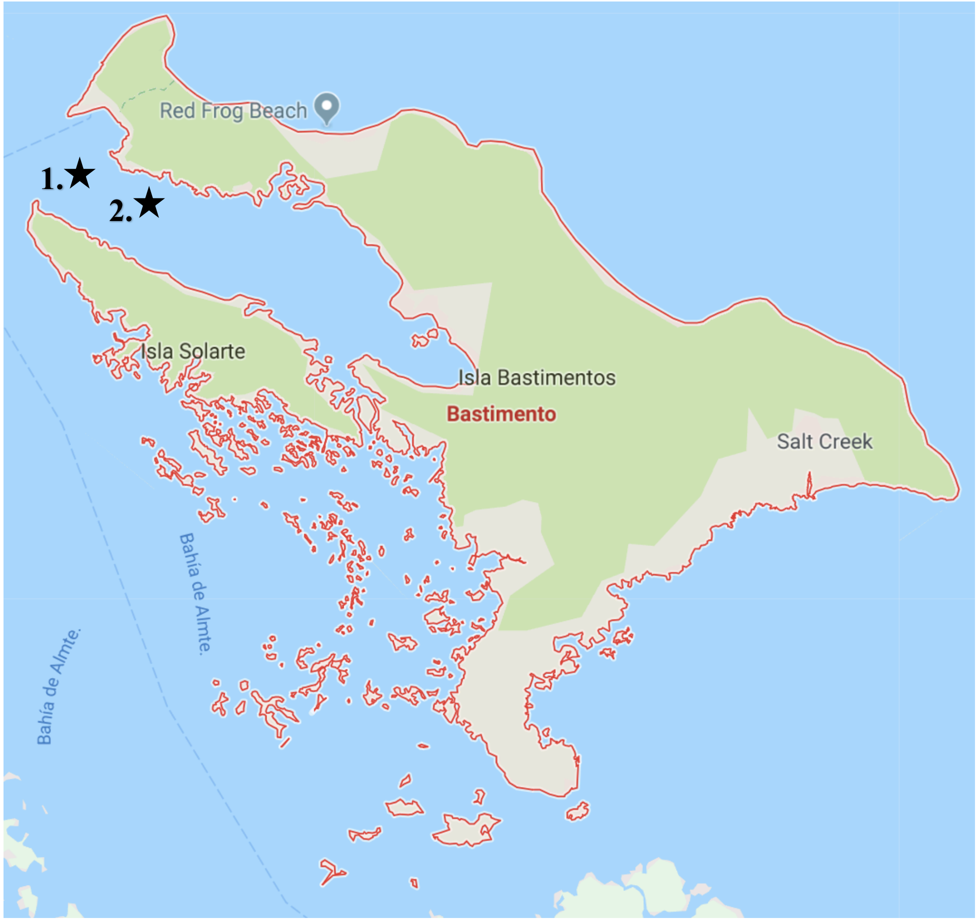

Figure 1. Study sites 1 and 2 (denoted by stars) located off of the western coast of Isla Bastimentos. Photo retrieved from Google Maps.

Data collection

Data was collected in the morning during the period after sunrise (roughly 6:45 am – 9:45 am GMT-5) and in the afternoon (12:45 pm – 3:45 pm GMT-5). The morning data collection typically occurred after the first high tide averaging approximately 0.2 m and before low tide of approximately 0.1 m. The afternoon data collection typically occurred after the moonset and low tide. The order in which the coral reef and seagrass transect data was collected was rotated for every collection to minimize any temporal separation between the two habitats. Beginning in either the coral reef or seagrass habitat, a tape measure was secured to the ocean floor with rebar at the first appropriate location. Two consecutive 15 m transects were laid in a random direction. Two more consecutive 15 m transects were laid down perpendicular to the first transects crossing at the middle to form the shape of a cross to be used for video data collection (Ibekwe et al. 2002) (Figure 2).

After a five to ten-minute fish recovery period, each 15 m transect was swum slowly in a random order with a Nikon Coolpix W300 waterproof digital camera to record a video until the camera malfunctioned, then a GoPro Hero 5 Black was used. After testing the camera at three different angles, pointed straight down (Willis et al. 2000), situated perpendicular to the bottom (Tessier et al. 2013), and 45° from the bottom, the camera was ultimately positioned at approximately 45° angle from the ground as that was able maximize the field of view and capture the most fish given the conditions of the study environment (Holmes et al. 2013). A video of the benthos and fish was recorded at a resolution of 1080 at 60 frames per second and with a linear field of view on the GoPro while swimming slowly with the transects in the middle of the frame serving as a marker and calibration tool (Watson et al. 2005; Assis et al. 2013). The video camera was pointed straight forward along the transect line the whole time and deviating the camera from the transect line was avoided to refrain from including fish that were present in a wider field of view than the one that was intended (Holmes et al. 2013). The videos were typically between 40 seconds and 1 minute and 10 seconds long given the water conditions and depth of the transects. The depths of each habitat as well as the percent coverage of seagrass in the seagrass beds were estimated at each site. This was repeated twice in each habitat and at two different times of day in each habitat. Data was collected two separate times at each of the two sites for a total of 16 transects per habitat per time of day per site.

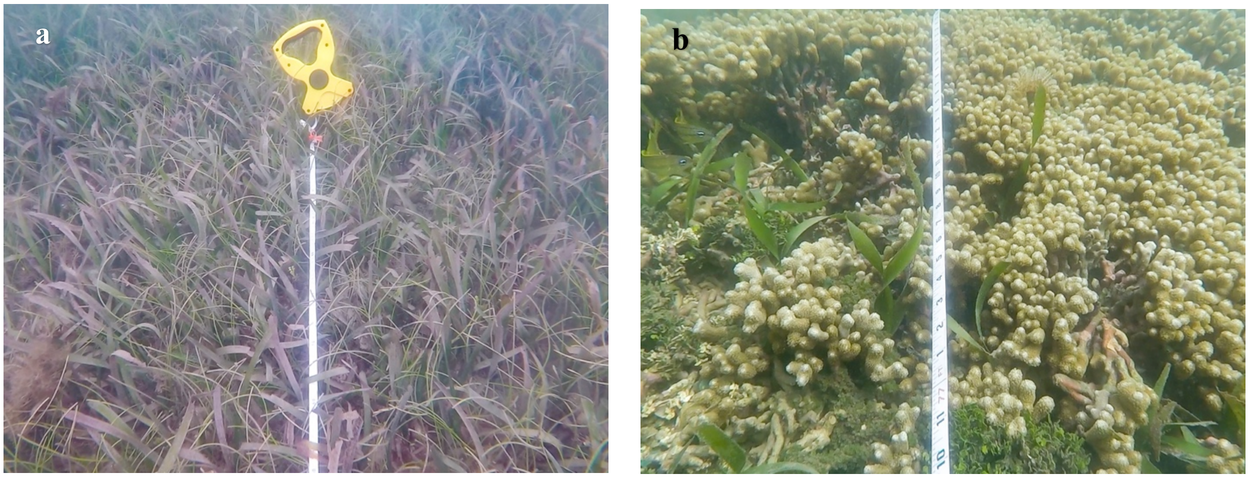

Figure 2. Examples of transect line in (a) seagrass and (b) coral reef. The fish located on the left side of (b) the coral photograph are *Haemulon plumierii* (White Grunt). Photos by Kathy Liu.

Data analysis: photographic

Two screenshots were taken from each of the coral reef videos and utilized as photoquadrats in order to survey the benthic substrate composition of the reefs (Green et al. 2008). When needed, the screenshots were uploaded onto Adobe Lightroom for basic adjustments such as color and lighting corrections as well as minor adjustments of exposure and contrast to increase the clarity of the substrate and to minimize dark areas (Iqbal et al. 2010). The photos were then cropped so that they all represented a quadrat of roughly 0.5 m x 0.5 m for the purpose of benthic substrate identification. The substrates were separated into the following large morphofunctional groups: scleractinian corals (brain, starlet, staghorn, lettuce, finger), hydrocorals (fire), sponges, macroalgae, seagrass, other organisms (urchins, anemones), substrate (sand, rubble), and dead coral for analysis (Martínez-Rendis et al 2016). The total percentage of each substrate group was calculated and averaged over all of the reef transects per site.

Data analysis: video

Raw video footage was uploaded onto Final Cut Pro X for Mac. They were edited with the "Balance Color" function on the program to correct for color and lighting (Shen 2016). The videos were played back frame by frame to count and identify fish down to a species level using the "Reef Fish Identification: Caribbean, Bahamas, South Florida" (Humann and Deloach, 2011) field guide and an online Caribbean marine organism identification guide (Snorkel St. John, 2018) as a reference. When possible due to morphological differences, fish were recorded as juveniles or adults.

Data analysis: statistical

The data was compared in multiple pairs of factors which will be referred to as F(#). Site 1 morning seagrass, Site 1 morning coral, Site 1 afternoon seagrass, Site 1 afternoon coral, Site 2 morning seagrass, Site 2 morning coral, Site 2 afternoon seagrass, and Site 2 afternoon coral were all compared accordingly (F1-F12). The following factors were also compared: Site 1 seagrass vs Site 1 coral (F13), Site 1 seagrass vs Site 2 seagrass (F14), Site 1 coral vs Site 2 coral (F15), Site 2 seagrass vs Site 2 coral (F16), Site 1 morning vs Site 1 afternoon (F17), Site 1 morning vs Site 2 morning (F18), Site 1 afternoon vs Site 2 afternoon (F19), Site 2 morning vs Site 2 afternoon (F20), seagrass morning vs seagrass afternoon (F21), seagrass morning vs coral morning (F22), seagrass afternoon vs coral afternoon (F23), coral morning vs coral afternoon (F24), seagrass vs coral (F25), and morning vs afternoon (F26). Shannon-Wiener and Simpson Diversity Indices were calculated for species abundance and evenness for each habitat and each time of day at each site. The Sorenson evenness coefficient was also calculated to compare species similarity for F13,16,17,20,21,24,25,26. Statistical one-way ANOVA, two-way ANOVA, and Hutcheson t-tests were also conducted to observe for significant differences between the habitats, times of day, sites, and Shannon Diversity Index values. Finally, the other data collected (habitat depth, and seagrass coverage) were averaged for each site.

Ethical considerations

This project was approved by the Local Review Board (LRB) and SIT Institutional Review Board (IRB). No human subjects were involved in this study, but steps were taken to ensure minimal harm and impact to the coral reef and seagrass habitats in which the study was conducted. The rebar stakes for the transect were placed in rubble or sand, making sure to not affect any live corals or other living organisms. No living organisms were removed from the environment and everything that was brought into the water in order to conduct the research was also removed from the water when data collection was finished each time.

Results

Site observations

Data was collected from Site 1 over a total of 5 days between November 10th and 18th, 2018. The weather was partially cloudy or overcast for the majority of the collection periods and it rained on a handful of the days during data collection. The temperature ranged from 26-29°C. The depth of the reef sampled was 1-2 m and the depth of the seagrass was also 1-2 m. The coverage of seagrass in the seagrass beds was roughly 75% with an average canopy height of approximately 15 cm. *Thalassia testudinum* was the prominent seagrass species and various types of macroalgae were highly present in the beds as well. The most abundant fish families were Antherinidae, Pomacentridae, Clupeidae, and Labridae while the most abundant species were *Hypoantherina harringtonensis*, *Stegastes diencaeus*, *Harengula humeralis*, and *Thalassoma bifasciatum* (Table 1).

Data was collected from Site 2 over a total of 3 days between November 14th and 17th, 2018. The weather varied from clear skies and sunny to overcast and sprinkling during the data collection times. The temperature also ranged from 26-29°C. The depth of the reef sampled was 1-3 m and the depth of the seagrass was 1-1.5 m. The seagrass beds had a coverage of about 65% and the average canopy height was approximately 25 cm. *Thalassia testudinum* was the prominent seagrass species and macroalgae was present although not as prevalent as in Site 1. The most abundant fish families were Haemulidae, Clupeidae, Scaridae, and Pomancentridae while the most abundant species were *Haemulon flavolineatum*, *Harengula humeralis*, *Scarus iser*, and *Haemulon plumierii* (Table 2).

Benthic composition

The benthic composition was averaged between two photoquadrats per each of the 32 coral transects and is shown and compared in Figure 3. Open substrate (sand and rubble) composed the largest percent (33.45%) of the sea floor of Site 1, while macroalgae composed the largest percent (32.22%) of Site 2 (Figure 3). The percent coverage of the other morphofuntional groups differ between sites with the exception of dead coral which is fairly even between the two sites covering 16.39% of Site 1 and 15.24% of Site 2 (Figure 3). The least plentiful group(s) were hydrocorals (fire coral) and other organisms (urchins, anemones) at Site 1 each making up 0.20% of the reef transects and in Site 2 the least plentiful group was sponges which made up 0.30% of the transects (Figure 3).

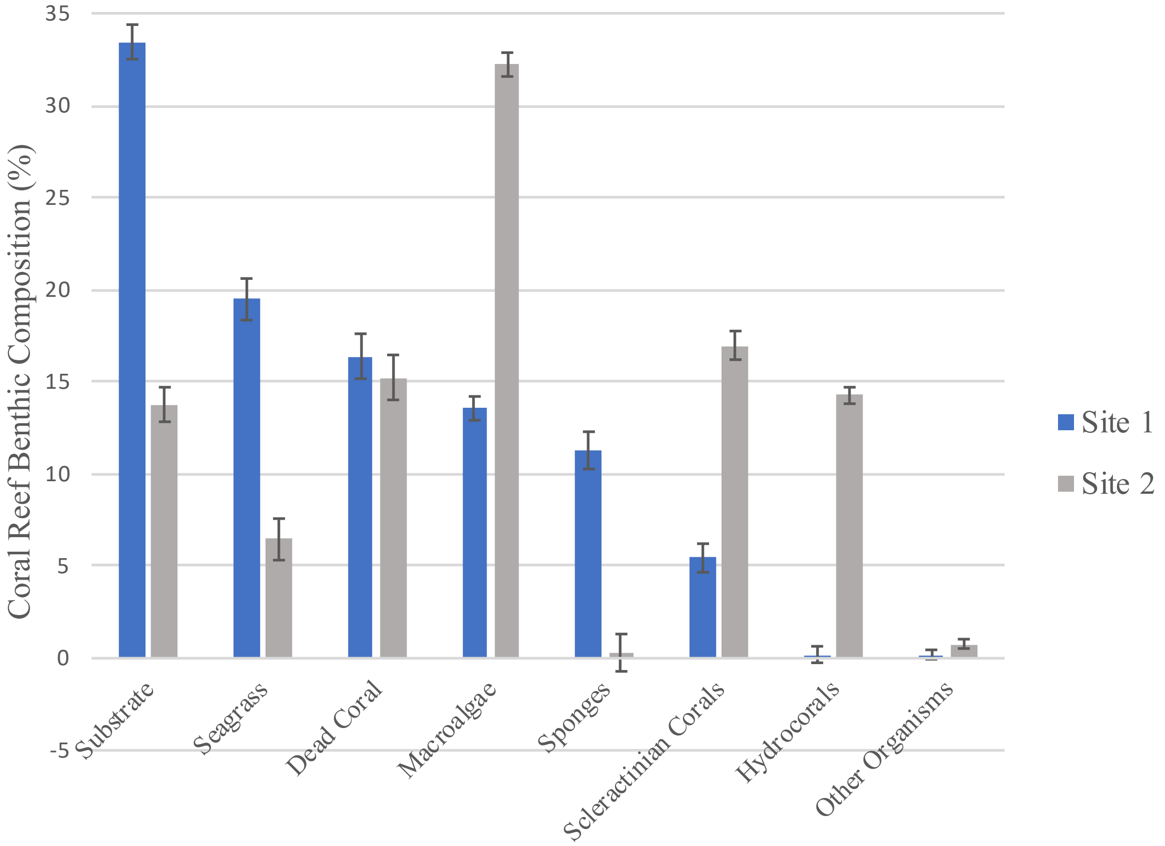

Figure 3. Average benthic composition percentages (+SE) of the coral reef at Site 1 and Site 2. (n=64 at each site) Note. Substrate representing coral rubble and sand.

Reef fish statistics: diversity, abundance, and evenness

A total of 3587 fish were observed using video recordings representing 14 different families and 32 different species across both sites. At Site 1, 2645 fish were observed (Table 1) and at Site 2, 942 fish were observed (Table 2). The total abundance and richness were calculated for the morning, afternoon, seagrass, and coral reef at each site (Table 3). One-way ANOVA tests were conducted for abundance and evenness of F1-F26 and no significant differences between the pairs were found. The smallest result was $F_{F16,\ 1,32}=0.09$, p=0.766 and the greatest was $F_{F19,\ 1,32}=1.40$, p=0.246. Although there was no statistically significant difference ($p>0.05$) found for comparisons F14, F15, F18, F19, it can be observed from the habitats (seagrass and coral reef) at each site that the seagrass at Site 1 was the most abundant (N=1637) but had the lowest richness with 9 species, and the coral at Site 2 was the richest with 22 different species (Table 3). It can also be observed from the times of day (morning and afternoon) at each site that the highest abundance was during the morning at Site 2 (N=1907) even though it had the lowest richness with 15 different species (Table 3). The afternoon at both sites had the highest richness with 18 different species at each site but were also the times with the lowest abundance ($N_{\text{Site 1}}=582$, $N_{\text{Site 2}}=359$) (Table 3).

Table 1. Abundance of fish species observed at Site 1 during the entirety of the study in each habitat at each time of day. Scientific and common names of the fish species are given. A one-way ANOVA was performed and there were no significant differences ($p<0.05$) found between total fish abundance values in each habitat at each time of day.
• denotes fish species observed exclusively in the coral reef and Δ denotes fish species observed exclusively in the seagrass

	Site 1			
	Morning		Afternoon	
Family/Species	Seagrass	Coral	Seagrass	Coral
SCARIDAE				
Scarus iseri (Striped Parrotfish)	28	17	13	48
Sparisoma viride (Stoplight Parrotfish)		5	4	1
HAEMULIDAE				
Haemulon aurolineatum (Tomtate) Δ	28			
Haemulon parra (Sailor's Choice)			3	3
Haemulon chrysargyreum (Smallmouth Grunt)			8	
Haemulon flavolineatum (French Grunt)		2		
LABRIDAE				
Halicoeres bivittatus (Slippery Dick)	5		5	4
Thalassoma bifasciatum (Bluehead Wrasse)	7	70	35	108
Halichoeres poeyi (Blackear Wrasse) •				2
CHAETODONTIDAE				
Chaetodon capistratus (Foureye Butterflyfish)		8	1	4
Chaetodon ocellatus (Spotfin Butterflyfish) •		2		5
POMACENTRIDAE				
Stegastes diencaeus (Longfin Damselfish)		178	4	145
Stegastes partitus (Bicolor Damselfish) •		3		
Microspathodon chrysurus (Yellowtail Damselfish) •		3		2
Abudefduf saxatilis (Sergaent Major) •		3		10
ATHERINIDAE				
Hypoantherina harringtonensis (Reef Silverside)		95	1500	
CLUPEIDAE				
Harengula humeralis (Redear Sardine)		270		10
LUTJANIDAE				
Lutjanus apodus (Schoolmaster) •		4		
ACANTHURIDAE				
Acanthurus coeruierus (Blue Tang) •		2		
Acanthurus tractus (Ocean Surgeonfish) •				1
Total	68	662	1569	346

Table 2. Abundance of fish species observed at Site 2 during the entirety of the study in each habitat at each time of day. Scientific and common names of the fish species are given. A one-way ANOVA was performed and there were no significant differences ($p<0.05$) found between total fish abundance values in each habitat at each time of day.
• denotes fish species observed exclusively in the coral reef and Δ denotes fish species observed exclusively in the seagrass

	Site 2			
	Morning		Afternoon	
Family/Species	Seagrass	Coral	Seagrass	Coral
SCARIDAE				
Scarus iseri (Striped Parrotfish)	3	60		42
Sparisoma viride (Stoplight Parrotfish)	1	16		3
HAEMULIDAE				
Haemulon chrysargyreum (Smallmouth Grunt)		4		
Haemulon flavolineatum (French Grunt)		180	1	171
Haemulon plumierii (White Grunt) •		20		64
LABRIDAE				
Halicoeres bivittatus (Slippery Dick)	3	2		
Thalassoma bifasciatum (Bluehead Wrasse)	24	3	10	7
Halichoeres garnoti (Yellowhead Wrasse)			1	
CHAETODONTIDAE				
Chaetodon capistratus (Foureye Butterflyfish)		4		2
Chaetodon ocellatus (Spotfin Butterflyfish) •		1		
POMANCENTRIDAE				
Stegastes diencaeus (Longfin Damselfish)	5	20	4	29
Stegastes planifrons (Threespot Damselfish) •				3
Abudefduf saxatilis (Sergaent Major) •		1		
Stegastes leucastictus (Beaugregory) •		18		5
ATHERINIDAE				
Hypoantherina harringtonensis (Reef Silverside)	60	16		
CLUPEIDAE				
Harengula humeralis (Redear Sardine)	134			
LUTJANIDAE				
Ocyurus chrysurus (Yellowtail Snapper) Δ	1			
Lutjanus apodus (Schoolmaster) •				2
Lutjanus synagris (Lane Snapper) •		1		4
Lutjanus mahogoni (Mahogany Snapper) •				1
SERRANIDAE				
Hypoplectus puella (Barred Hamlet)	1	2	1	3
GERREIDAE				
Ulaema lefroyi (Molted Mojarra) Δ			4	
ACANTHURIDAE				
Acanthurus coeruierus (Blue Tang) •		2		
HOLOCENTRIDAE				
Sargocentron curuscum (Reef Squirrelfish) •				1
TETRAODONTIDAE				
Sphoeroides testudineus (Checkered Pufferfish) •				1
GOBIIDAE				
Coryphopterus dicrus (Colon Goby) •				1
Total	232	350	21	339

Table 3. Summary data of fish abundance, species richness, diversity, and evenness for comparisons F14-15,18-19.

	Seagrass		Coral Reef		Morning		Afternoon	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Total abundance	1637	253	1008	589	730	1907	582	359
Richness	9	12	18	22	16	15	18	18
Shannon-Wiener Diversity Index (H)	0.42	1.36	1.76	1.87	1.77	0.87	2.01	1.71
Simpson Diversity Index (E_h)	0.16	0.65	0.78	0.76	0.77	0.38	0.82	0.72

The different habitats and times of day at each site had relatively low to moderate fish diversity given that the typical Shannon-Wiener Diversity Index value ranges between 1.5 and 3.5, rarely exceeding 4 (Table 3). When comparing the sites, the seagrass at Site 1 had the lowest Shannon Diversity Index (H=0.42) and evenness (E_h=0.16) in general while the afternoon at Site 1 had the highest Shannon Diversity Index (H=2.01) and highest evenness (E_h=0.82) (Table 3). After combining the data of the morning, afternoon, seagrass, and coral reef, the Shannon Diversity Index was calculated, graphed, and a Hutcheson t-test was used to compare the Shannon Diversity Index (H) value of F25 and F26 (Figure 4). The difference between H in the morning (H=2.09) and in the afternoon (H=1.35) is very statistically significant (p_{F26}=5.82E-68, ***$p<0.001$, df=3454). The difference in Shannon Diversity Index between the seagrass (H=0.77) and coral reef (H=2.18) is also very statistically significant (p_{F25}=3.60E-242, ‡$p<0.001$, df=3493). Sorenson's coefficient was calculated for F13, F16, F17, F20, F21, F24, F25, F26 and converted into percentages in order to evaluate fish species similarities between habitats per site, time of day per site, habitat per time of day, and between habitats and time of day overall. All of the comparisons ranged between 47.06% and 72.73%. The coral fish species during the morning and afternoon were most similar with a percentage of similarity of 72.73% while the seagrass fish species during the morning and afternoon were 54.55% similar. The percentage of similarity between seagrass and coral reef species of both sites combined is 54.55%. The species observed in the morning and afternoon data collection periods were 72.00% similar

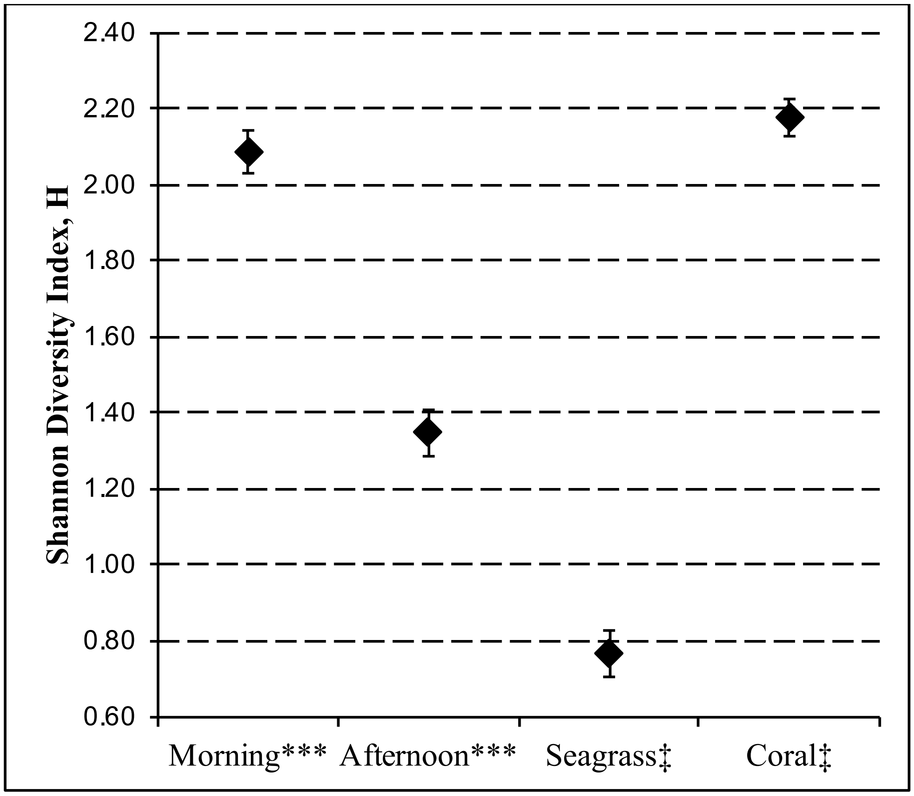

Figure 4. Graph of Shannon Diversity Indices (H) including error bars for comparisons F25 and F26. The difference between Shannon Diversity Index (H) of the Morning (H=2.09) and the Afternoon (H=1.35) is statistically significant (p=5.82E-68, ***p<0.001). The difference between Shannon Diversity Index (H) of the Seagrass (H=0.77) and the Afternoon (H=2.18) is statistically significant (p=3.60E-242, ‡p<0.001).

Relationship between habitat and time of day on fish diversity

Figures 5-7 show the total number of individuals within the given parameters. Figure 5 represents the total number of individuals present in each habitat at each site. One-way ANOVA tests were conducted for F13-16 resulting in no statistically significant differences but it can be observed that the total abundance is greatest in the seagrass at Site 1 (N=1637) (Figure 5). Figure 6 represents the total number of individuals present at each time of day at each site. One-way ANOVA tests were conducted for F17-20 resulting in no statistically significant differences but it can be observed that the total abundance is greatest in the afternoon at Site 1 (N=1907) (Figure 6). Figure 7 represents the total number of individuals present in each habitat at each time of day. One-way ANOVA tests were conducted for F21-24 resulting in no statistically significant differences but it can be observed that the seagrass afternoon had the greatest total abundance (N=1590) and the seagrass morning had the least total abundance (N=300) (Figure 7). When habitats and time of day were compared in a two-way ANOVA test (Table 4), no statistically significance was found in the variance as a result of both habitat and time of day as related factors.

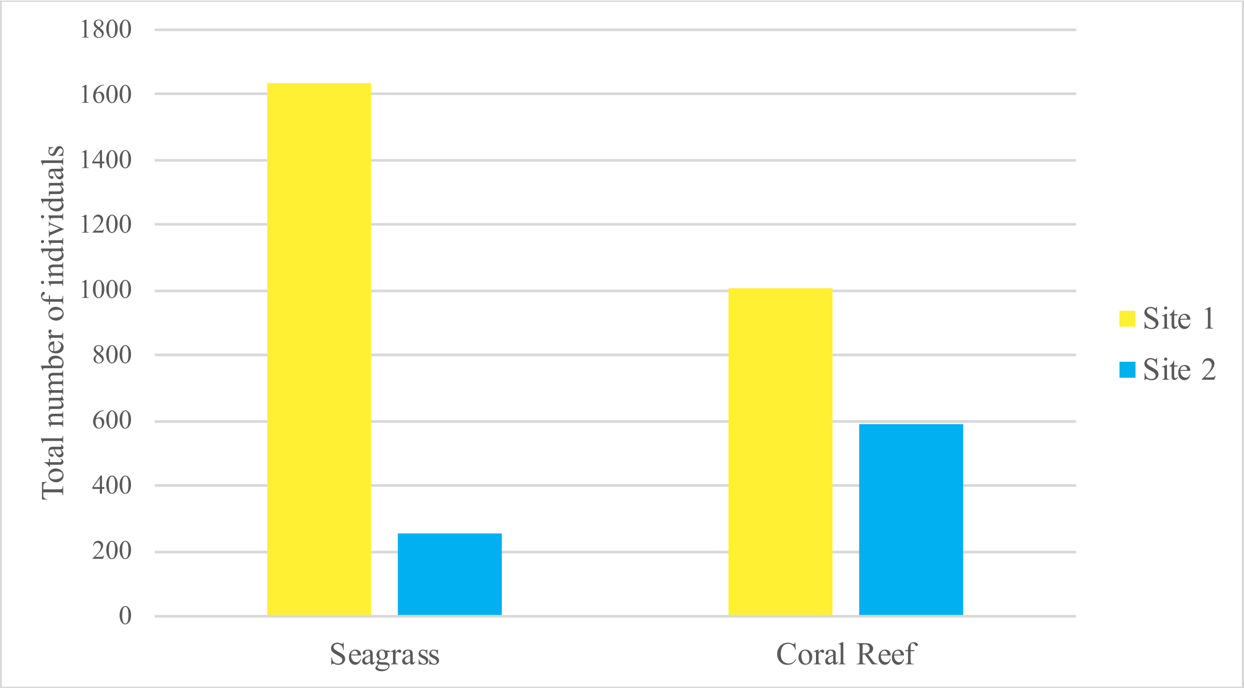

Figure 5. Total number of individuals present in each habitat at each site. No statistically significant differences (p<0.05) were found after conducting a one-way ANOVA test for comparisons F13-F16.

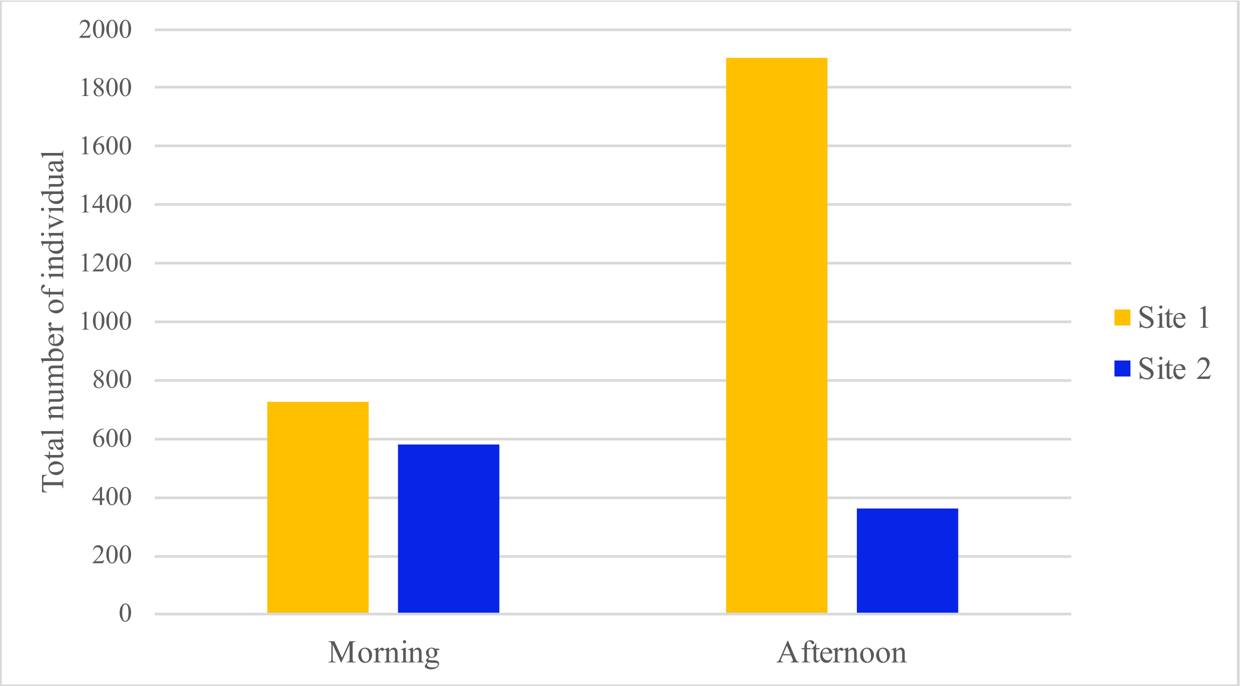

Figure 6. Total number of individuals present at each time of day at each site. No statistically significant differences (p<0.05) were found after conducting a one-way ANOVA test for comparisons F17-F20.

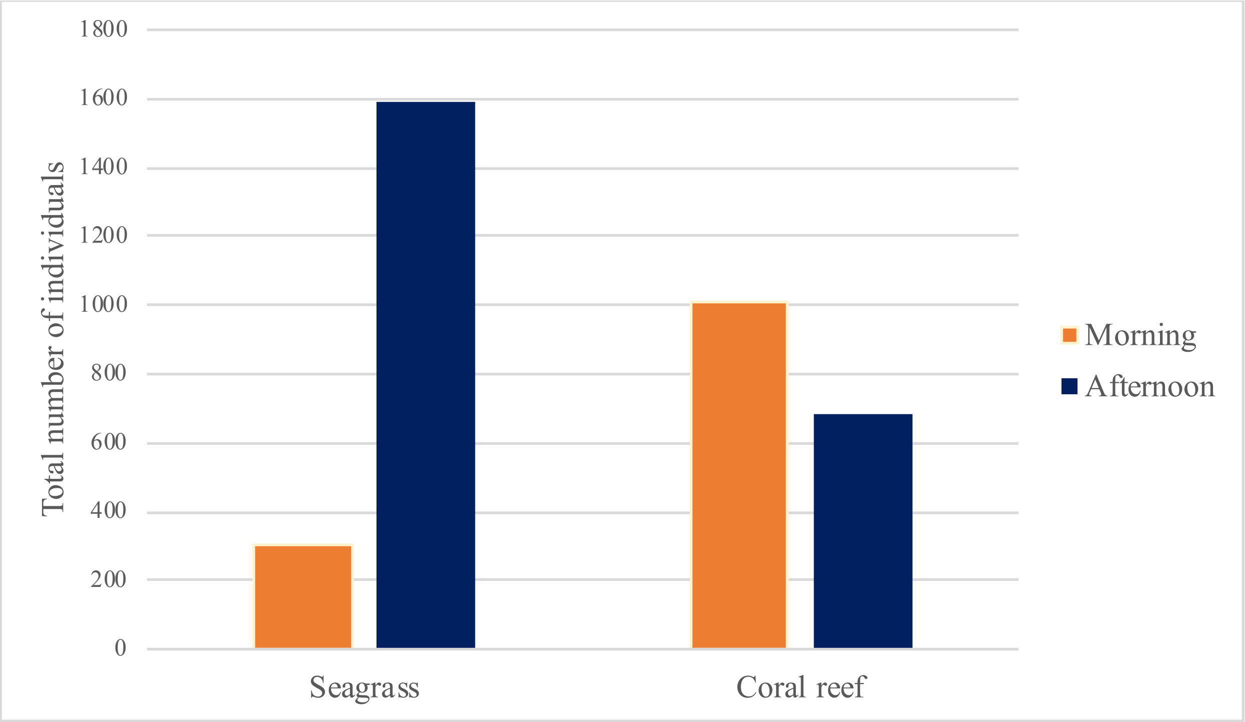

Figure 7. Total number of individuals present in each habitat at different times of day. No statistically significant differences (p<0.05) were found after conducting a one-way ANOVA test for comparisons F21-24.

Table 4. Analysis of variance between habitats (seagrass, coral reef) and time of day (morning, afternoon). No statistical significance (p<0.05) between habitat and time of day was found.

	df	MS	F	p
Habitat	1	12545.67	0.34	0.5621
Time of day	1	61542.17	1.67	0.2015
Habitat*Time of day	1	145913.62	3.95	0.0517
Error	57	36923.01		

Note. MS = Mean squares, *p<0.05, †p < .01. ‡p < .001.

Discussion

Site characteristics

Tropical reef fish were present in both the seagrass and coral reef throughout the day at both sites off the western coast of Isla Bastimentos in Panama. The seagrass coverage and canopy height did not differ greatly between the two sites and thus would not have had an effect on any differences between the results collected from the seagrass. At Site 1, the total live coral coverage was only 5.46% while Site 2 had a total live coral coverage of 31.24%, making live coral the second largest group covering the Site 2 transects after macroalgae which covered 32.22% of the transect. Site 1 had a generally greater total abundance of fish than Site 2 which could suggest that fish abundance is not correlated with percent live coral coverage, but these results could also be due to the small sample size of the study. Other studies (Gratwicke and Speight 2005) have also found that live coral coverage is not a significant indicator of fish species abundance or richness. Site 1 was more exposed to boat traffic, wave action, and currents than Site 2 was and was generally more abundant than Site 2 in each habitat and at each time of day which fit with hypothesis H_1 even though the results were not statistically significant. This is consistent with what Dominici-Arosemena and Wolff (2005) found regarding abundance increasing as exposure increases.

Because the light fluctuated throughout the study period each site due to varying cloud coverage, especially during the morning period, the termination of the transition period was difficult to determine. The variations in light can affect to what degree fishes are switching in the transition period and could affect the behavior and presence of fish species in the afternoon. Some diurnal fishes' activity also changes throughout the day in ways unrelated to transitioning (Hobson 1972). This study started data collection after sunrise and was not able to collect data before sunrise like other similar studies have done (Hobson 1972) which would be beneficial in future studies to better understand activity, abundance, and evenness of tropical reef fishes during the dawn to morning transition.

Reef fish species diversity, abundance, and evenness

The video surveys conducted during this study did not find significant differences between fish abundance or evenness between seagrass and coral reefs, between the morning and afternoon in either habitat, or between sites (F1-24). This means that the null hypotheses that there is no difference between samples have failed to be rejected. Although not statistically significant, a difference of fish abundance between habitats at each site can be observed (Figure 5). The observational difference between the seagrass and coral reef could be due to edge effects (Dorenbosch et al. 2005). Edge effects tend to occur in the transitioning area between coral reef and seagrass beds and depending on underlying mechanisms, can foster a difference in fish species abundance with better ecotone or transitions between ecosystems increasing diversity (Ries and Sisk 2004).

Generally, fish abundance was lower in the seagrass than the coral reef at each time of day at each site with the exception of the seagrass at Site 1 which had large schools of *H. harringtonensis* (n=1500). The extreme abundance of these small reef associated fish could potentially be skewing the total abundances and resulting in insignificant differences in total fish abundance and affecting typical evenness of the habitat. The Simpson Diversity Index (1-D) of the seagrass is 0.31 which means that there is a 31% chance that when two individuals are selected from the sample, they will be of different species. That is a low evenness as the range of Simpson values is from 0-1 with 1 meaning there is a 100% change that two individuals selected will be different species and that the sample is even. The Simpson Diversity Index of the coral reef is much higher at 0.85 meaning there is an 85% chance that two chosen individuals from a sample will be of different species.

The afternoon period generally observed a higher abundance of fish than the morning. This may be due to the fact that some diurnal fish take longer to become active to decrease predation risk during the transition period (Hobson 1972) and are not out and about until later in the day. Significant differences were found in the diversity between the morning and the afternoon and between the seagrass and coral reef. The Shannon Diversity Index (H) was significantly greater in the morning than the afternoon thus allowing hypothesis H_2 to be accepted. This also means that the null hypothesis, which states that there is no difference in fish diversity between morning and afternoon, can be rejected. The difference can be explained by the fact that morning collection period was during a transitional period where diurnal and nocturnal fish species are both out switching from foraging to finding shelter or vice versa (Hobson 1972). The Shannon Diversity Index (H) was also significantly greater in the coral reef than in the seagrass which confirms hypothesis H_3 to be correct and leads to the rejection of the null hypothesis stating that there is no difference in fish diversity between the habitats. Coral is more heterogenous and complex than seagrass often fostering a higher diversity of fish (Grober-Dunsmore et al. 2007; Schrandt and Lema 2011; Graham and Nash 2013) by offering more habitats, niches, and protection from predators thus more species were observed in the corals off the coast of Isla Bastimentos.

From the Sorenson evenness coefficients, it can be observed that the coral fish species during the morning and afternoon were most similar with a percentage of similarity of 72.73% while the seagrass species during the morning and afternoon were 54.55% similar. The percentage of similarity between seagrass and coral reef species of both sites combined is 54.55%. The species observed in the morning and afternoon data collection periods were 72.00% similar

Reef fish diets and life stages

A total of 1618 herbivorous fish, 41 omnivorous fish, and 231 carnivorous fish were observed in the seagrass. A total of 681 herbivorous fish, 94 omnivorous fish, and 922 carnivorous fish were observed in the coral reef. Herbivorous fish are able to obtain organic matter, living plant, and epiphyte biomass from the extremely productive seagrass beds (Heck Jr. et al. 2008) and that may be the reason that the greatest number of diurnal fishes in the seagrass were herbivores. These results are consistent with the findings of Robblee and Zieman (1984) but are also generalized to seagrass beds in close proximity to coral reefs. Coral reefs are also productive habitats but are able to better support more trophic levels since the structural complexity of the coral provides more homes to more marine organisms (Graham et al. 2017). Densities of specialized feeders have been found to increase in sheltered zones (Dominici-Arosemena and Wolff 2005) which in this study is Site 2. Herbivore and omnivore fish species densities were lower at Site 2 than Site 1, but carnivore fish species densities were higher at Site 2 with 647 carnivores than at Site 1 with 541 carnivores. These differences are not significant and cannot support the findings of Dominici-Arosemena and Wolff (2005).

Not all fish species display morphological differences between juveniles and adults and thus determining the relative age of an individual can be difficult without measuring biomass or capturing the fish for further inspection. The majority of the fish of the species that could be identified as juveniles or adults in both the seagrass and coral reef were juveniles.

*Possible sources of error and limitatio*ns

The study in general was limited by time and by the number of transects that were collected. Water depth and light penetration also limited data collection because as depth increased and/or light penetration decreased, the video resolution decreased which resulted in reduced visibility and increased difficulty observing and identifying fish species. Water visibility independent of water depth also hindered observations during the study. Heavy rains, increasing swells, and an upwelling decreased water visibility during multiple data collection times which meant that there could have been a lot of fish that were unable to be observed in the videos. Human error could have also impacted fish observations, fish identification, and benthic surveys from the videos. The videos were played back frame by frame, but some fish still could have been missed, especially the smaller fish and fish that camouflaged into the benthos, and larger schools of fish could have been miscounted. Fish populations also could not have been complete if the period waited after setting up the transects for fish recovery was not long enough.

Suggestions for further research

Future research on this topic should be conducted with the goal to better understand the effects of time of day, adjacent marine habitat connectivity, and habitat complexity on tropical reef fish diversity, abundance, and evenness. Along with more multivariable studies, more studies on the individual variables affecting the seagrass-coral reef continuum are necessary in order to better understand marine ecosystems, fish species, and behavior. Future studies could benefit from larger sample sizes including more transects, an increased number of sites, and/or an increase in data collection days at each site. Studies can also be conducted over multiple years to look for any long-term changes. Due to the difficulty of staying underwater and the reduced video quality at greater depths, future studies could utilize scuba to allow for greater time spent underwater and the inclusion of deeper habitats.

In regard to data collection, better, higher quality cameras can be utilized in order to take higher resolution videos at more frames/sec in order to get a more detailed analysis. Multiple cameras can also be combined at multiple angles in order to capture more fish. More in-depth analysis of the videos could also be done to be able to observe and identify fish. While underwater video recordings are an efficient tool to use in the field, they may not be the most accurate depending on the site specifics and the fish being studied, as smaller fish, cryptobenthic fish (Ahmadia et al. 2012), or those that may not be moving and do not clearly stand out in the videos may be overlooked.

Conclusions

The findings of this study demonstrate that time of day did not significantly affect reef fish abundance or evenness in the seagrass-coral reef continuum off the western coast of Isla Bastimentos in the Bocas del Toro archipelago in Panama. The null hypotheses of F1-F24 failed to be rejected. However, fish diversity was significantly different between the morning and the afternoon and between the coral reef and the seagrass bed, rejecting the null hypothesis of F25 and F26. This signifies that on a larger scale, time of day and habitat type separately affect diversity of reef fish in the study area.

Studying the importance of multiple habitats, such as seagrass and coral reefs, the effects they have on fish communities, and the effect they have on each other are important in cultivating better knowledge on the subject in the scientific realm. The roles they play on fish diversity and abundance are also important in the creation of Marine Protected Areas (MPAs) like the one located in Bastimentos, Isla Bastimentos National Marine Park. Fish community structures have shown clear difference in biomass, with fish of all trophic levels demonstrating equal or greater biomass in MPAs when compared to open all-access waters (Soler et al. 2015). Most MPAs only include the coral reef, but the seagrass beds and other reef related habitats also play an important effect on coral reef fishes in the tropics due to the connectivity between habitats (Dorenbosch et al. 2007; Unsworth et al. 2008) and should be include in MPAs as well (Heck et al. 2008).

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