Impacts of diving tourists on coral reef community structure and herbivorous reef fish foraging behavior

by

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Abstract

Increasing contact between humans and nature can disturb essential processes within ecosystems. Chronic anthropogenic disturbances on coral reefs may shift benthic community composition leading to loss of reef growth and biodiversity. The use of coral reefs for ecotourism can promote economic growth and conservation, if well managed. The presence of ecotourists has the potential to damage the benthic community through direct contact with corals and to disrupt foraging behavior by herbivorous fishes. I report here how reef community structure varies along a gradient of ecotourism use, and how tourist presence affects herbivorous reef fish behavior in the short- and long-term, on an intensively-visited portion of the Mesoamerican Barrier Reef. In Akumal Bay, Mexico, tourist use varied from low on reefs in the southwestern end of the bay, to very high (~ 1079 snorkelers per day) in the northeastern area of the bay. Reef-building coral cover decreased and macroalgal cover increased significantly with the level of tourism. Sea urchins exhibited species-specific trends related to tourism level. Neither the abundance nor diurnal foraging patterns of herbivorous fishes varied significantly with tourist abundance in the bay, suggesting a lack of long-term changes in fish behavior. However, they exhibited significant short-term responses to the experimentally-manipulated presence of divers. I recommend that reef managers should enforce carrying capacities for tourist use per day on coral reefs, to limit the types of ecosystem disturbances described here.

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Table of contents

List of Tables

List of Figures

Abbreviations

SCUBA	Self-Contained Underwater Breathing Apparatus
OPM	Optimal Patch Model with Multiple Costs
MABR	Mesoamerican Barrier Reef
CEA	Centro Ecologico Akumal
CCA	Crustose Coralline Algae
CMA	Erect Calcified Macroalgae
FMA	Erect Fleshy Macroalgae
YKS	Yal Ku Somero (SCUBA dive site)
HMBS	Half Moon Bay Somero (SCUBA dive site)
AKS	Akumal Somero (SCUBA dive site)
ESC	La Escuelita (SCUBA dive site)

Chapter 1

Thesis Introduction

Coral reefs around the world are growing in popularity as tourism destinations. The recent growth of ecotourism, an industry that promotes sustainable use of environments and cultures to boost the local economy and encourage appreciation for nature, has promoted the use of reefs for snorkeling and SCUBA diving tours in place of extractive practices such as fishing (Honey 2008). This type of potentially benign use of reef resources may lead to improved conservation and increased public awareness and appreciation of these tropical marine systems, than the extractive activities that currently occur on many reefs. Ecotourism on reefs can both promote biodiversity and be economically profitable, because SCUBA divers and snorkelers (hereon referred to collectively as "divers") are willing to pay higher prices to visit more biodiverse and healthy reefs (Wielgus et al. 2010). Divers perceive reefs as higher quality and more enjoyable to visit when there is high cover of live coral, diverse assemblages of both fish and corals, and more numerous schools of fish (Uyarra et al. 2009). However, paradoxically the physical presence of divers in a coral reef ecosystem may disturb the reef attributes that they prefer to see, and thus risk the survival of the local tourism industry by degrading the health of the reef system on which the industry depends

(Hawkins et al. 1999; Gil et al. 2015). In order for ecotourism to function well, the use of fragile systems, such as coral reefs, must be managed sustainably to maintain the ecosystem health that forms the foundation of this industry (Honey 2008).

Divers cause damage to living corals by fracturing their skeletons and abrading their delicate tissues, through inadvertently contacting corals with their fins, bodies, or other diving gear (Barker and Roberts 2004; Krieger and Chadwick 2013). This disturbance and physical damage weakens corals, making them more susceptible to predators and disease (van de Water et al. 2015), and reducing their ability to compete against algae for reef space (Rosenberg et al. 2007). Reef-building stony corals are in constant competition with macroalgae for substrate and dominance of the reef structure (McCook 2001; McClanahan et al. 2002). Natural disturbances, like hurricanes, are common on reefs and may temporarily shift species composition within the coral assemblage, but rarely push the system into a phase-shift in which macroalgae establish dominance on the reef (Connell 1978; Galzin et al. 2016). In contrast, chronic anthropogenic disturbances, like frequent diver damage, nutrient pollution, and overfishing, can overwhelm the system and reduce abundance of reef-building species (Connell 1978; McClanahan et al. 2002; Burkepile and Hay 2006).

Loss of herbivores and nutrient loading are posited as causes of algal overgrowth on reefs (Mumby et al. 2006); however studies have shown that removing herbivores is the more significant disturbance of the two relative to increasing algal biomass (Koop et al. 2001; Burkepile and Hay 2006). Physical removal of herbivores from a system by predation can release primary producers from grazing pressure and lead to changes in overall community structure. Equally though, an herbivore’s fear of predation can alter their foraging behavior enough to lead to a trophic cascade in the system without physical reduction in the number of herbivores; this is the concept behind the ecology of fear (Brown et al. 1999; Cherry et al. 2016). Brown (1988) expanded earlier optimal foraging models by defining an optimal patch model with multiple costs (OPM) that predicts the amount of time an organism will remain in a foraging patch based not only on available nutrients in the patch and travel time to the next patch, but also on additional costs such as potential predation risk in a patch, or the loss of mating opportunities due to time spent in the foraging patch (Nordell and Valone 2013). Based on the OPM and the ecology of fear one predicts that foragers may choose to abandon a foraging patch based on fear of predation without physically being preyed upon. These types of choices, in turn, can affect the structure of the ecosystem.

Humans are not directly factored into the OPM and the ecology of fear when we are not serving as true predators by hunting or fishing. If we are perceived as predators by mobile herbivores, even while partaking in non-threatening ecotourism activities like hiking or diving, we may inadvertently alter the foraging behavior of important ecosystem engineering herbivores in the environments that we visit. Coral reefs are an ideal model system for examining anthropogenic effects on herbivory, due to their ecological importance and ease of observation of herbivorous coral reef fishes, coupled with the increasingly-frequent exposure of these fishes to human presence. While ecotourism may reduce the removal of herbivores via overfishing, the physical presence alone of humans in reef ecosystems potentially can alter herbivorous fish foraging behavior if they fear divers, resulting in a major reduction in macroalgal control similar to an overfishing effect.

I describe here the impacts of rapidly growing ecotourism on the coral reefs of Akumal Bay, Quintana Roo, Mexico, in terms of both direct physical damage to corals by divers, and also indirect effects on macroalgal vs. coral cover due to potential behavioral disturbance of herbivorous fishes. Akumal Bay contains a portion of the Mesoamerican Barrier Reef (MABR), the second largest reef tract in the world spanning much of the coastline along the western edge of the Caribbean Sea (see map, Chapter 2). Coastal tourism has been increasing for decades in the Mexican state of Quintana Roo, which parallels the MABR (Torres and Momsen 2005, Fig. 2.1 in Chapter 2). Quintana Roo's popularity with tourists began with the conception of Cancun as a pre-planned tropical tourism destination (Torres and Momsen 2005). As Cancun's popularity with tourists outgrew it's physical carrying capacity as a city, the industry moved further south to the less congested towns of Playa del Carmen and Cozumel. Playa del Carmen is currently the fastest growing city in Mexico (B. Figueroa, pers. comm., Centro Akumal Ecologico). As Playa del Carmen crowds with tourists, the industry once again is expanding further south along the coast towards Akumal, where rapid growth can be seen over the last year alone in the form of new Americanized restaurants and a new, expansive luxury hotel on the beach (B. Renfro pers. obs.). The rapid but recent growth of the ecotourism industry centered around the corals and sea turtles of Akumal Bay, makes the bay an ideal place to study the effects of tourist presence on the coral reef ecosystem, and provide information to implement sound management before the reef is degraded past a point of possible resiliency in the system.

The main street of Akumal Town contains the majority of the tourism infrastructure and is located along the northeastern section of the bay, causing tourists to enter the beach area from the northeastern corner, and to mostly remain in the north bay. This geography creates a gradient of both on-land beach use and in-water snorkeling activity, that I used to examine differences in the benthic community structure and diurnal fish behavior associated with varying levels of tourism pressure. Snorkeling tours are concentrated in the northern half of the bay and SCUBA diving is not permitted within the bay so dive boats take SCUBA divers just off shore to forereef patches outside the reefcrest. This separation of diving activities allowed me to examine not only the effects of diver presence on herbivorous fish foraging behavior but also potential differences in disturbance from the two types of recreational activities (snorkel vs. SCUBA) that are popular in Akumal. In 2016, Akumal Bay was declared a refuge for protected marine species, including sea turtles, by PROFEPA (The Federal Attorney for Environmental Protection under the Mexican Government), enhancing the need for scientific information to manage human activities in this ecosystem (DOF 2016).

Chapter 2 of this thesis examines variation in benthic coral reef community structure along a tourism gradient in Akumal Bay, and Chapter 3 explores the related effects of tourist presence on herbivorous fish behavior on these reefs. The overall goals of these studies are to document various effects of the ecotourism industry on coral reefs in Akumal Bay, and to provide guidance for the sustainable management of this new marine refuge, as well as for coral reef tourism destinations worldwide.

Chapter 2

Variation in coral reef community structure with recreational snorkeling levels in Akumal, Mexico

Abstract

Chronic anthropogenic disturbances on coral reefs may shift benthic community composition away from reef-building corals and toward dominance by macroalgae, leading to reduced reef growth and biodiversity. The use of coral reefs for ecotourism activities can limit such disturbances while promoting economic growth, but may cause negative ecological impacts if not well-managed. I report here how coral reef community structure varies along a gradient of ecotourism use, on an intensively-visited portion of the Mesoamerican Barrier Reef. In Akumal Bay, Mexico, levels of recreational snorkeling were quantified in 6 sections of the bay, and levels of beach use by tourists were quantified in 4 adjacent sections on land. The percent cover of major benthic organisms, including species of reef-building corals and major types of macroalgae, were quantified on selected patch reefs in each of the 6 bay sections. Tourist use varied from very low in the southwestern end of the bay, to very high (~ 1079 snorkelers per day) in the northeastern corner of bay, where abundant sea turtles attract tourists. Overall reef-building coral cover decreased and macroalgal cover increased significantly with the level of snorkeling tourism. Two relatively resistant corals (*Montastraea annularis* and *Porites porites*) were “winners”, in that their percent cover increased significantly with tourism level, while 3 sensitive corals (*Diploria strigosa, Agaricia tenuifolia* and *Acropora palmata*) were “losers” with decreased cover in intensively-visited portions of the bay. Sea urchins also exhibited species-specific trends in relation to tourism level. These results indicate that intensive ecotourism appears to be shifting the benthic reef community toward dominance by macroalgae and relatively few species of hardy corals and sea urchins. We conclude that limitation of rates of visitation, coupled with in-water management of snorkeler (and diver) behavior, are needed to prevent severe degradation on these and other coral reefs exposed to intensive tourism, especially as the popularity of reef-based ecotourism continues to grow.

Introduction

Background: Disturbance on coral reefs

Coral reefs are fragile ecosystems in which reef-building corals compete both among themselves and with other non-reef-building organisms for dominance of the benthic community (Chadwick and Morrow 2011). Natural disturbances on healthy coral reefs, such as storms, may alter the species composition of benthic organisms, but usually do not shift the system away from reef-builders (Connell 1978; Galzin et al. 2016). In contrast, chronic anthropogenic disturbances can overwhelm the system and reduce the abundance of reef-building species (Connell 1978; McClanahan et al. 2002). Macroalgae are major competitors for space with reef-building corals on tropical reefs (McCook 2001; McManus and Polsenberg 2004), and are prevented from becoming dominant through the activities of grazing fishes and sea urchins (Mumby 2006a). In addition, naturally low levels of dissolved nutrients also control macroalgae (Littler et al. 1991; Miller and Hay 1996). Dominance on coral reefs also can be shifted toward algae and away from corals through human activities such as overharvesting of herbivorous fishes and excessive use of fertilizers or dumping of sewage along adjacent coastlines (Burkepile and Hay 2006).

Background: Mesoamerican Barrier Reef

The Mesoamerican Barrier Reef (MABR) is the second largest contiguous coral reef tract in the world. This reef spans much of the coastline along the western edge of the Caribbean Sea, bordering the entire coast of southeastern Mexico from the northern tip of the Yucatan Peninsula, to the eastern coastlines of Belize, Guatemala and Honduras (Fig. 2.1a). Coastal tourism has been rising for decades in the Mexican state of Quintana Roo, which parallels the MABR (Torres and Momsen 2005, state and reef location shown in Fig. 2.1). Quintana Roo's popularity with tourists began with the conception of Cancun as a pre-planned tropical tourism Mecca (Torres and Momsen 2005). Continuing growth of human activity associated with the tourism industry has expanded the human population of the state of Quintana Roo >15-fold over the past 40 years, to ~1.5 million in 2013 (INEGI 1970, 2013). Most of this population is concentrated along the coastline, especially in the cities of Cancun (within the coastal municipality of Benito Juaréz, 2010 population > 600,000) and Playa del Carmen (> within the coastal municipality of Solidaridad, population 150,000, INEGI 2010). With the overdevelopment of Cancun (Torres and Momsen 2005), the tourist industry recently has expanded down the coastline to less congested towns. Akumal (within the coastal municipality of Tulum, 2010 population just over 28,000, INEGI 2010) is ~105 km south of Cancun, and contains a portion of the MABR that is experiencing rapidly-growing coral reef tourism, partly due to its resident sea turtle population which attracts busloads of snorkeling and diving tourists daily (Gil et al. 2015). Coral reefs in the most intensively-visited portions of the bay are beginning to show signs of degradation (Gil et al. 2015). More detailed information concerning benthic community structure of Akumal's coral reefs and how it varies with levels of snorkeling tourism is needed to support the management of sustainable levels of tourism in this unique bay, which is one of the major feeding and nesting areas for green and loggerhead sea turtles in the Yucatan (Molina Hernández and van Tussenbroek 2014). Coral species composition and relative abundances in the bay remain unknown, and yet these data are important to provide baseline values for tracking potential changes as tourism continues to increase, especially in low-use areas of the bay that are not yet visited frequently by tourists. In 2016, Akumal Bay was declared a refuge for protected marine species, including sea turtles, by PROFEPA (The Federal Attorney for Environmental Protection under the Mexican Government), enhancing the need for scientific information to manage human activities in this ecosystem (DOF 2016).

Present Study:

Ecotourism has been hailed as a solution to ecosystem degradation related to extractive uses such as fishing and mining, because it incentivizes the preservation and non-destructive human use of natural ecosystems (Honey 2008). The development of ecotourism on coral reefs is potentially an ideal way for tropical countries to use their diverse marine resources while avoiding extractive processes that degrade those resources. However, sustaining the economic benefits of an ecotourism industry requires regulation of the number of tourists who visit a given natural habitat each year, and of their actions as they interact with the ecosystem (Brown et al. 1997; Shi 2005; Iliopoulou-Georgudaki 2016). Tourists are willing to pay more to visit healthy versus degraded coral reefs, and will avoid damaged reef areas if given the choice (Wielgus et al. 2010), providing economic incentives for communities to manage their reef areas to maintain ecosystem diversity. Tour groups that are properly managed via snorkeler and diver education, coupled with dive guide surveillance, cause significantly less damage to coral reefs than do less-managed visitors (Krieger and Chadwick 2013). However, in many regions coral reef tourism is unregulated and intense, causing degradation that risks collapse of both the ecosystem and the local ecotourism industry (Gil et al. 2015).

When snorkelers’ and divers’ fins, bodies, or other diving gear accidentally contact corals they cause damage to living corals by fracturing their skeletons and abrading their delicate tissues (Barker and Roberts 2004; Krieger and Chadwick 2013). This disturbance and physical damage weakens corals, making them more susceptible to predators and disease (Guzner et al. 2010; van de Water et al. 2015), and reducing their ability to compete against algae for dominance (Rosenberg et al. 2007). Tourist presence also potentially reduces the abundance of herbivorous fishes on coral reefs (Gil et al. 2015), as well as their grazing activities (see Chapter 3). Herbivores play a major role on reefs by consuming macroalgae and thus reducing their ability to compete for space with corals (DeLoach 1999). Reefs that experience a severe reduction in herbivory transition to an alternate stable state dominated by algae instead of healthy scleractinian corals (Hughes 1994; McManus and Polsenberg 2004).

Reduction in the abundance of herbivorous fishes may also cause an increase in the abundance of sea urchins through competitive release, because these groups both consume algal food sources on the reef (Aronson and Precht 2000). Sea urchins serve an important, redundant role as major herbivores along side herbivorous fishes (Carpenter and Edmunds 2006). Reefs where either herbivorous fishes or urchins have been removed by overfishing or disease were able to maintain coral dominance with the presence of the redundant herbivore group but these systems collapsed when the second herbivore group was also removed (Hughes 1994). Urchins, however, are also capable of hard coral degradation in addition to algal maintenance, due to their scraping behaviors that remove coral spat along with algae from reefs, and thus they have potential for intensive bioerosion of reef substrate (Bak 1994). High abundances of sea urchins could ultimately cause damage to the reef ecosystem (Bak 1994; Cabanillas-Terán et al. 2016), thus urchin population size may impact reef resilience positively or negatively. Careful assessment of urchin abundances is important when considering the cascade effects of human disturbance on coral reefs.

Here I quantify how benthic community structure on patch reefs in Akumal Bay varies with levels of snorkeling and beach use by tourists. I then discuss how these results can be used to provide a scientific basis for the implementation of sustainable reef management practices to support the local ecotourism industry, during the currently expanding use of this reef system. These results can be applied to the management of reefs experiencing similar tourism use world-wide.

Methods

Study Sites

The present study was conducted during May to July 2015 at Akumal Bay, Quintana Roo, Mexico (20°24'00"N, 87°19'16"W, Fig. 1a). The bay contains coral patch reefs of various sizes, intermixed with sand and sea grass beds, and has a fairly continuous reef crest that extends along the mouth of the bay (also described in Mutchler et al. 2007; Gil et al. 2015). The reef crest protects the bay from high levels of water motion, creating a shallow inner bay area that usually has calm waters and thus attracts large numbers of snorkeling tourists (Molina Hernández and van Tussenbroek 2014). Most of the tourism infrastructure as well as the main street of Akumal town are located along the northeastern section of the bay, causing tourists to enter the beach area from the northeastern corner, and to mostly remain in the north bay. This geography creates a gradient of both on-land beach use and in-water snorkeling activity, from high in the northeast (~357 tourists in the water and on the beach at 15:00; 15:00 is an hour of high beach and bay use) to low in the southwest region of the bay (< 65 tourists in the water and on the beach at 1500 h, Gil et al. 2015). Based on preliminary observations, I thus partitioned the beach (on-land) area into 4 sections of approximately equal distance (~200 m, A-D), and the in-water area into 4 adjacent inner bay backreef sections, as well as two outer bay sections along the reef crest (E-J, Fig. 2.1b). Within each of the 4 inner bay areas, I then selected 2 patch reefs for benthic sampling based on their similarity in size (~150 m^2 area), depth (1.3 to 1.7 m deep), and distance from shore (~ 125 to 194 m from shore), to ensure that reefs exposed roughly similar physical conditions were sampled within each region of the bay (reefs #3-10 in Fig. 2.1b). In addition, I selected 1 patch reef for sampling in each of the 2 outer-bay reef crest sections (E and F, Fig. 2.1b), which were similar to each other in size (~ 150 m^2 area), depth (2.6 to 3 m deep), and distance from shore (~ 264 to 309 m from the shoreline, reefs #1-2 in Fig. 2.1b). Only 1 site in each outer-bay section was sampled due to low live coral cover from previous physical damage related to hurricanes Emily and Wilma, which damaged much of the Yucatan coastline in 2005 (Alvarez-Filip 2009; Mulcahy et al. 2016).

Patterns of tourist abundance

To quantify temporal and spatial patterns in the abundance of tourists both on the beach and in the water, I recorded their abundances during 6 periods each day for 5 days, in all 10 bay sections: 4 beach, 4 inner bay, and 2 outer bay (Fig. 2.1). The 5 dates for conducting tourist abundance surveys (July 10, 12, 26, 29, 30) were selected because they were sunny, and relatively low levels of floating algae *Sargassum* sp. (UNAM Reef

System Unit 2015) were present on the beach to obstruct tourist entry into the water. As such, the tourist levels reported here likely represent maximal values per day during the summer season in 2015.

On each of the 5 selected dates, a field assistant and I walked the entire length of the beach (section D to A) at the beginning of every other daylight hour between sunrise and sunset (times = 06:00, 08:00, 10:00, 12:00, 14:00, 16:00, 18:00; N = 6 periods total per day, duration of observations = the first ~ 10-20 min per 2-hr period). As we walked, one observer counted all tourists on each section of the beach, while the other simultaneously counted all tourists visible (wading, floating, swimming, or snorkeling) in the adjacent inner-bay water section. This practice avoided double counting of any tourists who moved between the beach and water areas during a given period.

Patterns of coral reef benthic community structure

To assess benthic community structure on patch reefs in the bay, I quantified all major components of the benthos at 10 patch reef sites (#1-10, Fig. 2.1). On each selected patch reef, I deployed 10 line transects parallel to shore each 10-15 m in length (depending on patch reef shape), spaced parallel to each other 1 m apart (adapted from Dickens et al. 2011), beginning at the near-shore edge of the reef. Along each transect, 3 points were chosen using a random number generator, then at each point, a 1-m^2 quadrat gridded with string to contain 100 10-cm^2 cells was laid gently on the reef surface (each cell is 1% of total benthic cover under quadrat). The identity of each type of substrate within each cell was recorded (3 quadrats per transect x 10 transects per reef = 30 samples per reef, modified after Hawkins et al. 1999; Krieger and Chadwick 2013; Mantelatto et al. 2013). Each benthic component was categorized as either: (1) stony coral, (2) macroalgae, (3) other sessile organisms, and (4) non-living substrate. Stony corals were broken into 14 species: *Agaricia agaricites, A. tenuifolia, Diploria clivosa, D. strigosa, Montastraea annularis, M. cavernosa, M. faveolata, Porites asteroides, P. divaricata, P. furcata, P. porites, Siderasterae siderae, Acropora cervicornis, A. palmata* (most common species, pers. comm. Baruch Figueroa-Zavala and preliminary observations), plus a category of "other" for less common corals. Macroalgae was broken into 4 types: crustose coralline algae (CCA), erect calcified macroalgae (CMA), erect fleshy macroalgae (FMA), turf, (after Stuhldreier et al. 2015). Other sessile organisms included: gorgonians, fire coral *Millepora*, sponges, sea anemones, zooanthids, or sea grass (after Oliver et al. 2014; Stuhldreier et al. 2015). Finally, non-living substrate was broken into sand, rubble, dead coral not colonized by turf algae.

In each sampled quadrat, I also assessed the abundances of sea urchins (long-spine sea urchins *Diadema antillarum,* and other less-common sea urchins grouped together, after Jordán-Garza et al. 2008). If more than half the body area of a given sea urchin occurred within the quadrat, it was counted as present within the quadrat (after Carpenter and Edmunds 2006).

Data Analyses

To statistically analyze patterns of tourist abundance, I focused on the peak-use periods of 14:00 on the beach and 16:00 in the water (see Results), to reveal patterns during the maximal-use periods each day. Tourist abundances were not normally distributed among days (Shapiro-Wilk normality test), so I employed a Generalized Linear Model (GLM) assuming a Poisson distribution for count data with R version 3.1.3 (R Core Team 2015), to determine whether tourist abundance varied significantly among sections of the bay, both on the beach and in the water. The Poisson regression assumption of equidispersion was verified using the dispersion test in R package AER. In cases where over dispersion was found, the model was re-fit with quasipoisson distribution to account for the data dispersion pattern. Post-hoc comparisons to determine differences in tourist abundance between each pair of bay sections were made using Tukey's Honest Significant Difference (HSD) test, using R function Simultaneous Tests for General Linear Hypotheses.

To statistically test for patterns in benthic community structure across the 10 examined patch reefs, I averaged percent cover estimates from the 3 quadrats examined per transect, to obtain a mean percent cover of each benthic category for each of the 10 transects per reef (N = 10 samples per reef). Then the 10 reefs were ranked from low to high in terms of their exposure to levels of tourist abundance in each water section of the bay, and benthic cover in each category was regressed on tourist level rank for each reef site, by fitting an ordinary least squares regression (OLS) in R. Residuals were examined using residual v fitted, normal Q-Q, scale location and residuals v leverage plots. Data were transformed where necessary to fit model assumptions. All results are presented as means +/- one standard error, unless noted otherwise.

Results

Patterns of tourist abundance

In the morning, tourist abundance was low and not significant among bay sections (Fig. 2.2). Tourist numbers increased toward afternoon to maximal values at 14:00 on the beach and 16:00 in the water, when they differed significantly among sections, both on land and in the water (GLM, on-land: $t = 9.63, 3.48, 3.22, 7.28$ for sections A-D respectively, $p < 0.001$ for all sections; in-water: $t = 1.05, 1.26, 1.53, 3.50, 4.18, 5.59$ for sections E-J respectively, $p = 0.14\text{-}0.30$ for E-G low use sections and $p < 0.001$ for H-J high use sections), and then declined toward sunset. Lowest use in-water sections (E-G), made up the majority of the in-water group and thus did not differ significantly from the group, but did differ significantly from the higher use sections via pairwise comparisons.

During the hour of peak on-land tourism occupancy at 14:00, tourist abundance in section D (where the public accessed the beach from the main road in town) was significantly higher than in all 3 other beach sections (Tukey's HSD test, $p < 0.001$, Fig. 2.2, Table 2.1). In contrast, sections C and B, the middle sections where the beach transitions from a public to a private area, contained moderate tourist abundances that did not significantly differ from each other ($p = 0.98$). Section A (private beach for a large resort hotel with limited access for general tourists) possessed significantly lower tourist abundances than did the other 3 beach sections ($p < 0.01$ for pairwise comparisons, Fig. 2.2, Table 2.1).

Overall, abundances of tourists in the water were lower than those on the beach, but indicated intense visitation of patch reefs in the bay. There were 187-343 tourists in the most intensively-visited water section during the hour of peak visitation (section J at 16:00); and total of ~1,000 people visited this section per day (section J, 06:00-18:00, Fig. 2.2). In the southern and outer sections of the bay, in-water tourist abundances during peak visitation at 16:00 were low and did not differ significantly from each other (E, F, and G, $p = 0.14$-0.30). These sections each averaged < 10 tourists in the water at 16:00, for a total of < 36 tourists per day. The middle sections of the inner bay contained moderate abundances of tourists, which differed significantly from all other in-water abundances, but not from each other (I and H, $p = 0.14$), while abundance at the northernmost in-water site was significantly higher than at all other in-water sites (J, $p < 0.001$ for all comparisons, Table 2.2). These patterns indicate that in-water tourist abundances varied significantly both with time of day, and with inshore-offshore as well as distance from public access point gradients in the bay.

Patterns of coral reef benthic community structure

Overall, live stony coral cover was low on patch reefs in the bay compared to algal cover, ranging only between 4.0-19.4% cover for corals, while macroalgal cover was higher, ranging between 55.0-85.9% cover. All other substrate categories (other benthic organisms, sea grass, etc.) ranged between 14.5-28.3% cover (range of mean cover in each category, N = 10 patch reefs). Live stony coral and macroalgal cover were inversely related; coral cover decreased significantly with tourist abundance, while macroalgal cover increased significantly (Fig. 2.3, Table 2.3).

Patterns of stony coral cover varied among coral types. Mounding corals as a group occupied the most space on the reefs (range of means = 1.5-9.9% cover, N = 10 reefs) and did not vary significantly with tourist abundance. Corals with branching and plating (foliaceous) morphologies covered less reef area than mounding corals (range of means = 0.21-7.67% cover branching, 0.35-5.57% cover plating), and decreased significantly with increasing tourist abundance (Fig. 2.4, Table 2.3). While mounding corals as a group showed no trend with changes in tourist abundance, individual species of mounding corals showed significant trends: symmetrical brain coral *Diploria strigosa* decreased significantly in percent cover with increasing tourist abundance, while boulder star coral *Montastraea annularis* increased significantly (Fig. 2.5, Table 2.3). At the species level, the negative regression for plating and branching corals was significant for both branching elkhorn coral *Acropora palmata* and foliaceous thin leaf lettuce coral *Agaricia tenuifolia*, while the branching finger coral *Porites porites* increased significantly with increasing tourist abundance (Fig. 2.5, Table 2.3). All other species of stony corals did not show significant trends. Each of the other 3 major types of sessile cnidarians (zoanthids, fire corals *Millepora* spp., gorgonians) all decreased significantly with increasing tourist abundance (Table 2.3).

The type of macroalgae that covered the most area on patch reefs in Akumal Bay was turf, followed by relatively low cover of erect calcified macroalgae (CMA), (range of means = 21.50-73.27% and 0.33-9.73% cover, for turf and CMA respectively, N = 10 patch reefs), with the other 2 algal types being even rarer. CMA and turf algae both increased significantly with tourist abundance on the reefs, though CMA only slightly so. Crustose coralline algae (CCA) and erect fleshy macroalgae (FMA) decreased significantly (Fig. 2.6).

Long-spined sea urchins *Diadema antillarum* occurred at abundances of 0-3 individuals m^{-2} and were most common on the offshore and southern bay sites; they decreased slightly, but significantly with tourist abundance (Fig. 2.7). Two other species of sea urchins (*Arbacia punctulata* and *Eucidaris tribuloides*) both had short robust spines, and were less abundant than *D. antillarum*, occurring at 0-2 individuals m^{-2}. They both exhibited the opposite trend of slightly, but significantly increasing abundance with tourism level (Fig. 2.7, Table 2.3).

Discussion

This study reveals that intensive rates of snorkeling tourism occur on some patch reefs in Akumal Bay, Mexico, and that live coral cover decreases linearly with snorkeling level, while macroalgal cover increases. These results suggest that the extremely high rates of snorkeling tourism in some parts of the bay (> 1,000 visitors per day) appear to negatively impact many of the reef-building corals, causing these reefs to enter a phase shift in which they become macroalgal-dominated, as has occurred in other reefs exposed to intensive human impacts (Hawkins et al. 1999; Muthukrishnan and Fong 2014). Gil et al. (2015) demonstrated that growing tourism in the bay is affecting both the benthic and fish communities; my results build on these findings by examining changes in the benthic community at a finer level, and revealing continued change in the level of tourist use throughout the bay.

Both the abundance and distribution of snorkeling tourists in Akumal Bay are expanding with increasing popularity of the site as a unique tourist destination, in which visitors can see both coral reefs and frequently encountered resident sea turtles. Rates of snorkeling tourism in the high-use area of Akumal Bay at peak use time each day doubled in 2015 (present study) compared to the numbers reported in 2013 (Gil et al. 2015; high-use area: mean number of people in the water at peak use time of day = 176 in 2013, 346 in 2015). The data revealed even more rapid growth of tourism in the low-use area of the bay, representing ~ 400% increase in 2 years (mean = 14 people in 2013, 58 in 2015, using the bay regions from Gil et al. 2015). Even more recent observations at Akumal indicate that snorkeling rates in the bay have continued to grow (B. Renfro, pers. obs., Centro Ecologico Akumal unpublished data). These results indicate trends in tourism growth, as well as continued alteration and degradation of benthic community structure on these coral reefs. They reveal intensive disturbance to the reef benthos along a gradient of human activity, however this bay is early enough in its development as an ecotourism destination, that if these trends are urgently addressed, both the live coral cover and the ecotourism industry that depends on it can be preserved.

With the recent completion of the new Secrets Akumal Luxury Hotel along the middle section of this bay, the once clearly high- versus low-use areas of the bay (Gil et al. 2015) are now expanding into a very high use section at the northeast end, moderate and growing use across the middle portion of the reef, and a shrinking section of low use toward the reef's southwest end. The Centro Ecologico Akumal (CEA) has designated a

U-shaped snorkeling route for tourists in the northeast end of the bay (sections I and J in Fig. 2.1), which is posted on maps at the northeast beach area where most tourists enter the water. This route was designed to concentrate human-reef contact in that end of the bay, thereby relieving snorkeling pressure on patch reefs in the remainder of the bay (aligning with the high and low use areas of Gil et al. 2015). However, due to lack of government enforcement, the routes are not followed and currently the total number of tourists entering the bay is not regulated. The results of the present work reveal that high levels of tourist use that have expanded into the mid section of the bay (section H, Fig. 2.1), and the associated degradation of coral cover now is found not only in sections J and I, but also in H.

The recent shift in reef community structure in Akumal Bay from reef-building coral dominance to algal dominance is expected to result in reduced biodiversity, due to reduced space for coral species to settle, and reduction in the calcareous reef structure, which provides habitat for myriad reef species and is the functional basis of the coral reef ecosystem (Jones et al. 2004; Graham et al. 2006).

The observed increase in percent cover of the mounding coral *Montastraea annularis* with the level of snorkeling tourism is interesting, given the decline of this species recently throughout the Caribbean Sea (Edmunds and Elahi 2007; Bruckner and Hill 2009; Edmunds 2010). At Akumal Bay, mounding corals appear to be resilient to tourism impacts, much more so than the structurally-delicate branching and plating (foliaceous) corals (Gil et al. 2015, Fig. 2.4). Colonies of *M. annularis* alter their reproductive strategies to clonally reproduce more in areas of high disturbance (Foster et al. 2013), which could potentially boost the percent cover of this species where tourists disturb the benthos. Recent work at St. John, U.S. Virgin Islands, shows similar trends of increased, but localized recruitment of *M. annularis,* supporting the idea that the species is potentially resilient and recovering in some areas of the Caribbean (Edmunds et al. 2011). It was equally unexpected that the percent cover of *Porites porites* increased with tourism level. This is a small branching coral, which often are considered to be fragile and easily broken when kicked or bumped by divers (Krieger and Chadwick 2013). Despite its relatively fragile morphology, *P. porites* is beginning to dominate disturbed reefs in other parts of the Caribbean (Greenstein et al. 1998). It belongs to a genus of weedy corals, and its rapid growth rate may permit *P. porites* to quickly colonize space opened by the decline of other coral species due to disturbances and so allowing the species to be a “winner” on rapidly changing reefscapes (Davies 1990; Edmunds 2010).

Currently mostly-dead skeletons of *Acropora palmata* dominate the reef-crest and deeper portions of the back-reef in Akumal Bay (B. Renfro, pers. obs.). *A. palmata*, and other Acroporids, once dominated reefs throughout the Caribbean (Adey 1978). However recently this group of species has been in decline due to compounding influences of anthropogenic and natural disturbances (Larson et al. 2014; Croquer et al. 2016). This trend, combined with the damage in Akumal Bay from hurricanes in 2005, explains the decrease in cover of *A. palmata* with increasing tourist levels in the bay (Macintyre et al. 2007). It should also be noted that *A. palmata* is typically found in reef crests and not backreefs as is seen here (Macintyre et al. 2007). *Agaricia tenuifolia,* however, has been referred to as a weedy species known to take over reefs where acroporids have died off (Chornesky 1991; Aronson et al. 2014; Cáceres and Sánchez Muñoz 2015). Interestingly, *A. tenuifolia* is not taking over the reef at Akumal, but instead exhibits decline with levels of tourism-related anthropogenic pressure. *A. tenuifolia,* commonly referred to as thin leaf sea lettuce for its leafy appearance, has a fragile plating morphology, so breakage from being kicked by tourists may outpace the rapid skeletal growth of this species (Chornesky 1991; Hasler and Ott 2008). Similar to *A. tenuifolia, Diploria strigosa* symmetrical brain coral, though not a weedy coral, has been predicted to dominate reefs as a "winner" in the face of growing anthropogenic disturbance (Flood et al. 2005; Edmunds 2010), but was observed here to decline with increasing tourism pressure. *D. strigosa* larval settlement is affected by algal assemblages (Miller et al. 2009), lending to the possibility that the increased algal cover in some sections of the bay may deter *D. strigosa* recruitment.

The increases observed here in turf algae and erect calcified macroalgae (CMA) with tourism levels have also occurred on other intensively-visited reefs, and are attributed to the decline of their competitors the stony corals (Hughes 1994) or to reductions in herbivory (McCook 2001; McManus and Polsenberg 2004). We also have demonstrated that the foraging behaviors of herbivorous fishes in Akumal Bay are disturbed by the presence of snorkelers, potentially releasing macroalgae from grazing pressure and enhancing their ability to overgrow corals (Chapter 3). Conversely, crustose coralline algae (CCA), which provide important substrate for juvenile corals to settle, exhibited a reduction in percent cover with level of human impact, similar to the pattern observed in studies on other reef systems (Smith et al. 2016). Fleshy macroalgae including *Laurencia* also declined here with tourism pressure, which was unexpected, given that they typically increase with human disturbance on coral reefs, as the system shifts to become macroalgal-dominated (Graham et al. 2015). One explanation for the inverse pattern observed here is that some damselfishes (common in Akumal Bay, Baruch Figueroa-Zavala unpublished data) exclude fleshy macroalgae in order to farm the turf algae that they prefer to consume (Casey et al. 2014). Some damselfishes chase away larger herbivores such as parrotfishes in order to protect their turf algae (Sammarco 1983; Casey et al. 2014). Because diving tourists also disturb the foraging behaviors of parrot- and surgeonfishes (Chapter 3), they may inadvertently allow resident damselfishes to instead devote their time to more thoroughly clearing out undesired fleshy macroalgae from their territories, and thus promote the growth of turf algae at the expense of large fleshy macroalgae on intensively-visited reefs.

Sea urchins serve a redundant role as major herbivores on coral reef systems, along with herbivorous fishes, but throughout the Caribbean Sea, the long-spined sea urchin (*Diadema antillarum*) which was once the dominant urchin species, has experienced a mass die off due to disease (Lessios 1988). This species is in recovery in some areas (Miller et al. 2003; Carpenter and Edmunds 2006), including Mexico (Jordán-Garza et al. 2008), but my results show that diving tourism may inhibit that recovery, as we observed fewer *Diadema* on more frequently-visited patch reefs. These sea urchins were common at my reef crest sites, however, possibly due in part to the abundance of *A. palmata* skeletons that provide these large urchins with better crevice habitats than the shallow inner bay sites. The other urchins observed in the bay were the smaller purple urchins (*Arbacia punctulata*) and slatepencil urchins (*Eucidaris tribuloides*), which both increased significantly with increasing tourism levels, possibly due to release from competition with herbivorous fishes for their algal food in the areas where tourists disturbed fish foraging. The 2 major types of reef foragers that would be expected to be most sensitive to visual disturbance (fishes, Gil et al. 2015) or habitat loss due to coral breakage (long-spined urchins *Diadema antillarum,* present study) by divers, are the types which declined with diving tourism levels. In contrast, the 2 smaller-bodied sea urchins that may not require highly-complex reef habitat (ie: which can fit into small crevices), did not decline in our study with tourist levels.

The significant declines observed here with tourism level for fire corals, gorgonians and zoanthids indicate that these 3 types of reef cnidarians may be sensitive to the reef disturbances caused by intensive snorkeling activity. The trend for gorgonians was only marginally significant. Some previous studies have shown that gorgonians are not affected by anthropogenic disturbance (Oliver et al. 2014; Lyons et al. 2015), while others have observed diver impacts on sea fans (Chadwick-Furman 1997). The reduced fire coral cover with tourist pressure was expected, because they possess delicate, easily-fractured skeletons and tend to respond to disturbance similarly to the scleractinian corals (Lewis 2006), as they are easily broken by divers (Chadwick-Furman 1997; Zakai and Chadwick-Furman 2002). Zoanthids also showed a marginally significant negative relationship with tourism level, but the mechanisms causing this trend are not clear; as a group, zoanthids do not show clear trends with anthropogenic disturbance (Yang et al. 2013; Cruz et al. 2015; Santos et al. 2015). Long-term studies are needed to assess changes in zoanthid cover along diver-use gradients.

While the addition of sites of low tourist-use along the reef crest eliminates possible arguments for solely a north-south gradient affecting benthic cover in the bay, there are possible alternative factors, in addition to diving tourist pressure, which could be affecting the benthic community at Akumal. The Yucatan peninsula is one of the most extensive karst aquifer systems in the world containing a labyrinth of ground water filled caves and cenotes, which empty freshwater into the Caribbean sea (Bauer-Gottwein et al. 2011). Freshwater seeps occur in Akumal Bay; groundwater can collect excess nutrients from terrestrial runoff throughout the entire watershed and deposit it onto coastal reef systems (Umezawa et al. 2002). Nutrient loading on reefs affects reef organisms and processes and specifically reduces coral growth and causes coral death at high nutrient levels (Koop et al. 2001). Patch reefs near ground water seeps in Akumal Bay may be negatively affected by added nutrients, however, Mutchler et al. (2007) found no differences in nutrient concentrations in Akumal Bay compared to less developed areas along the Quintana Roo coast, suggesting that submarine groundwater discharge may be fairly uniform along the coast on a short term time scale. On the scale of years, however, Akumal Bay has seen fluctuations in nitrogen stable isotope concentrations found in the gorgonian sea fans that correspond to fluctuations in year to year tourist visitation to the bay (Baker et al. 2013). Groundwater discharge in the bay may have variable effects on the benthos depending on the number of people visiting Akumal year to year.

Akumal also contains organized boating lanes and mooring zones in the north end of the bay. Boat noise disrupts larval coral reef fish settlement (Holles et al. 2013), and chemicals and heavy metals used in antifouling paints and boat cleaning agents leach into the surrounding water and cause damage to the reef ecosystem (Saphier and Hoffmann 2005). Sequestering of boat traffic to the northern bay may disturb the fish and benthic community in addition to the intensive snorkeling tourism in that area.

The data presented here highlight areas of concern about trends in the community structure of coral reefs in Akumal Bay, and associated tourism levels. Especially troublesome is the trend of temporally increasing tourism pressure in the highest-use areas of the bay. The benthic degradation recorded here on reefs in area J strongly suggests that this growing level of tourism currently exceeds the coral reef's tourist carry capacity, which in other studies has been set at 5000-6000 guided divers per reef site per year (Zakai and Chadwick-Furman 2002 and references therein). Snorkeling paths and no-snorkeling zones already set by CEA need to be enforced by government officials. If enforced, these regulations can help limit further spread of reef degradation in the bay and allow areas outside the snorkeling zones, but currently in-use by tourists to recover to the baseline state seen in the lowest use sections of the bay.

In addition to enforcing snorkeling and non-snorkeling zones, all hotels should encourage guests to participate only in guided dives and restrict snorkel gear rental to individuals entering the water with a guide. Tour groups utilizing highly educated guides that conduct pre-dive briefings and manage tourist behaviors in-water cause significantly less damage to reefs than less well-managed groups (Krieger and Chadwick 2013). The use of local guides will also add to Akumal's success as an ecotourism destination; ecotourism is not only defined as causing limited impacts on the environment, but also as boosting the local economy and limiting damage to the local culture (Honey 2008). Akumal's local dive guides are passionate about their reef resource and are more committed to regulating dive tourist behavior in order to protect reef organisms than are the non-local guides (Bobbie Renfro pers. obs.).

The design of mapped snorkel tour routes, the total number of guided snorkel tours permitted in the bay per day, and the total number of people per tour group all should be carefully examined and altered to reach these carrying capacity and regulatory goals. Akumal Bay was officially decreed a refuge for protected marine species by the Mexican government on 7 March 2016 (DOF 2016). This governmental support hopefully will be accompanied by the necessary enforcement of regulated tourist numbers and snorkeling routes, to more sustainably manage future tourism in the bay. Further scientific monitoring of the reef benthos and fish communities is necessary to continue to direct these management efforts.

Tables and Figures

Table 2.1. Simultaneous Tests for General Linear Hypotheses results. Z values and P values for post hoc pairwise comparisons of mean number of people in each section of beach along Akumal Bay at 14:00h.

		Increasing tourism ➔		
		A	B	C
↓ Increasing tourism	B	Z = 3.481 P = 0.00274	--	--
	C	Z = 3.220 P = 0.00629	Z = -0.346 P = 0.98472	--
	D	Z = 7.282 P < 0.001	Z = 6.198 P < 0.001	Z = 6.417 P < 0.001

Table 2.2. Simultaneous Tests for General Linear Hypotheses results. Z values and P values for post hoc pairwise comparisons of mean number of people in each section of water in Akumal Bay at 16:00.

		Increasing tourism ➔				
		E	F	G	H	I
↓ Increasing tourism	F	Z = 1.263 P 0.76855	--	--	--	--
	G	Z = 1.533 P = 0.59242	Z = 0.363 P = 0.99891	--	--	--
	H	Z = 3.496 P =0.00485	Z = 3.622 P =0.00297	Z = 3.496 P =0.00475	--	--
	I	Z = 4.181 P < 0.001	Z = 4.884 P < 0.001	Z = 4.887 P < 0.001	Z = 2.343 P =0.14491	--
	J	Z = 5.588 P < 0.001	Z = 7.506 P < 0.001	Z = 7.827 P < 0.001	Z = 8.349 P < 0.001	Z = 7.042 P < 0.001

Table 2.3. Summary of ordinary least squares (OLS) analyses on benthic cover data.
^ Data log$_{10}$-transformed, † Data square root-transformed

Response	R^2	SE	T	P
Live Hard Coral^	0.09698	0.01250	3.244	0.00161
Mounding Coral†	0.001625	0.03782	0.399	0.69
Branching Coral†	0.08639	0.03357	-3.044	0.003
Plating Coral†	0.08541	0.03405	-3.025	0.00317
A. agaricites	0.01502	0.06694	-1.222	0.2245
A. tenuifolia†	0.0764	0.03402	-2.847	0.00537
D. clivosa	0.007792	0.003454	-0.877	0.382
D. strigosa	0.1454	0.06443	-4.084	< 0.001
M. annularis†	0.05956	0.03594	2.491	0.0144
M. faveolata†	0.02085	0.03564	1.445	0.1517
M. cavernosa	0.03263	0.03000	-1.818	0.0721
P. asteroides†	0.001509	0.020522	-0.385	0.701
P. divaricata	0.004319	0.02479	-0.652	0.5159
P. furcata	0.003664	0.05468	-0.600	0.5497
P. porites†	0.1156	0.009455	3.579	< 0.001
S. siderae	0.003432	0.03373	-0.581	0.563
A. cervicornis	0.008608	0.03942	-0.922	0.359
A. palmata	0.07595	0.1448	-2.838	0.00552
Other hard coral	0	0.020925	-0.092	0.9271
Millepora	0.1455	0.04861	-4.085	< 0.001
Gorgonians†	0.04106	0.04204	-2.048	0.0432
Total Algae	0.205	0.4968	5.027	< 0.001
Turf Algae	0.4582	0.5366	-9.104	< 0.001
CMA†	0.07272	0.03675	2.772	0.00667
FMA†	0.102	0.0306	-3.336	0.0012
CCA†	0.254	0.05463	-5.776	< 0.001
Zoanthids	0.04461	0.01898	-2.139	0.0349
D. antillarum†	0.07113	0.02291	-2.739	0.00731
Other Urchin†	0.1436	0.018105	4.053	< 0.001

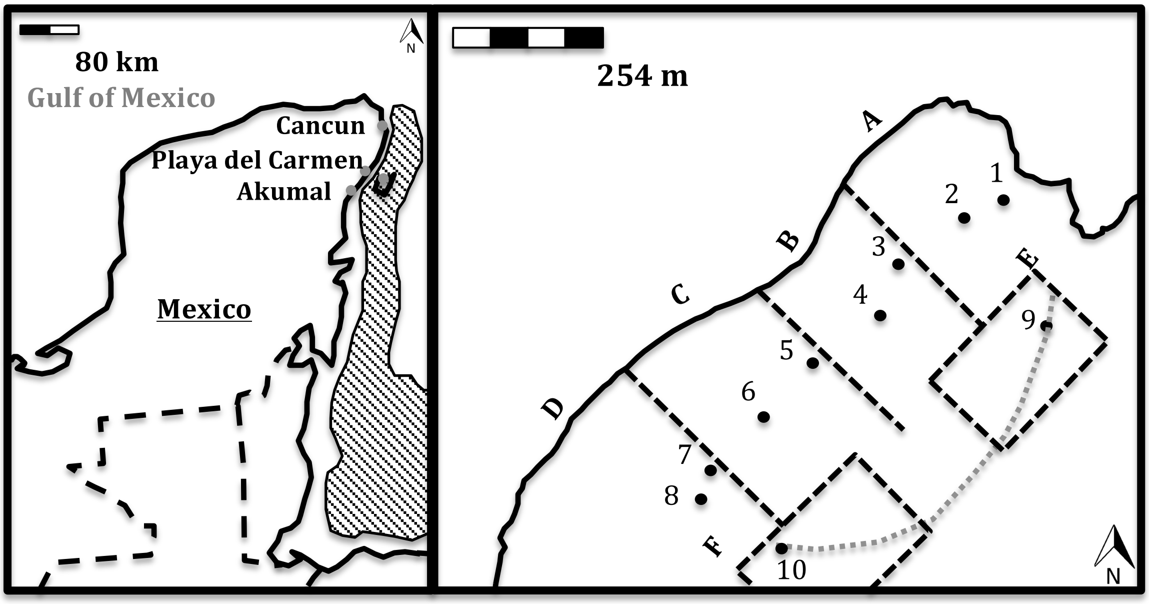

Figure 2.1a (left): Map of the Yucatan Peninsula; shows major tourist cities/towns in the northern Yucatan, including the study area of Akumal. The full extent of the Mesoamerican Barrier Reef is shown in the hatched section, including the adjacent coastlines of Mexico, Belize Guatemala and Honduras. 2.1b (right): Map of Akumal Bay. Letters and areas delineated by dashed lines represent regions used to quantify tourist abundance on the beach and in the water. Numbers indicate study reefs for benthic and fish surveys. Grey dotted line denotes the reef crest.

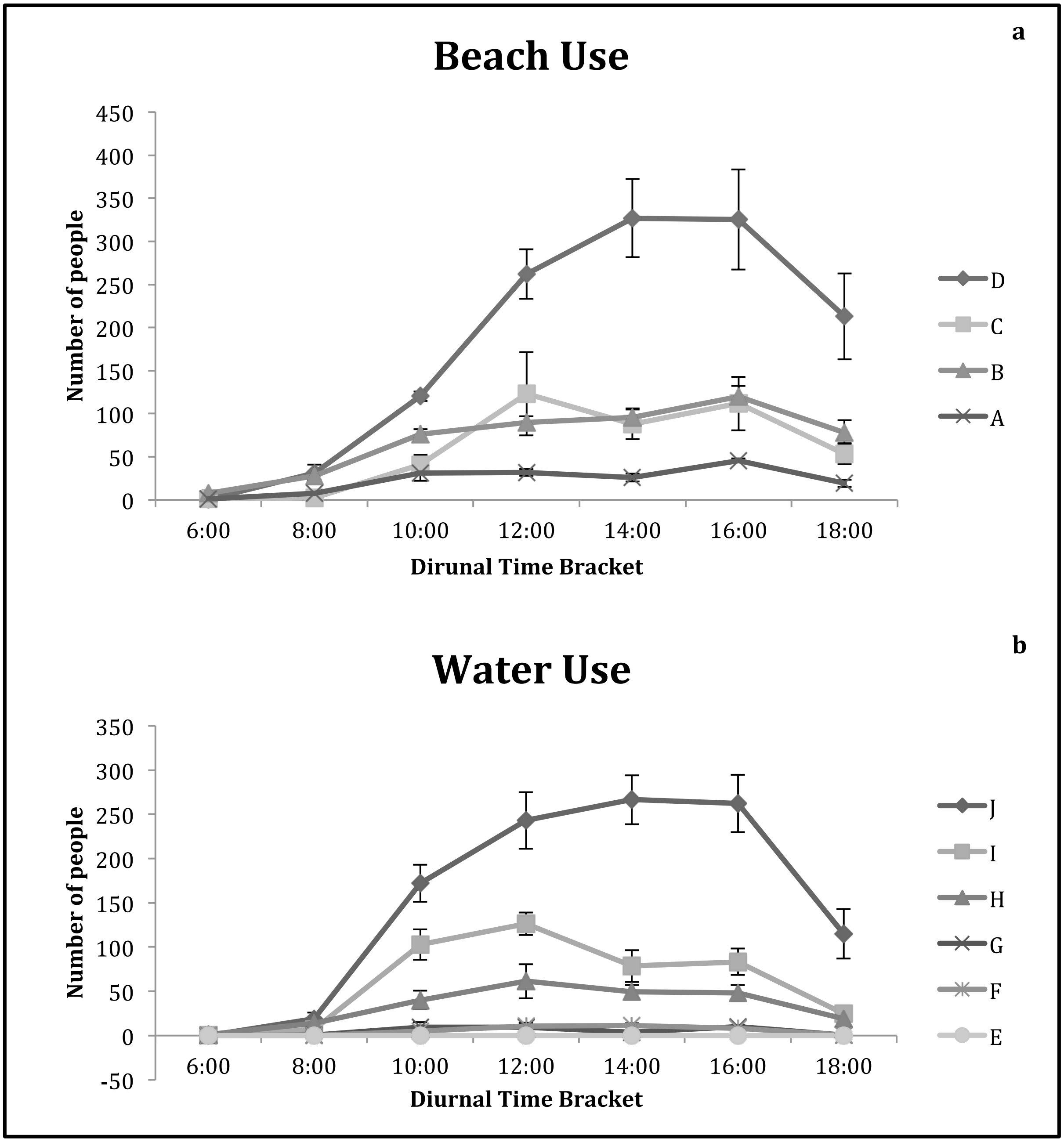

Figure 2.2. Variation in tourist abundance with time of day in Akumal Bay, Mexico, between (a) Four on-land (beach) sections, and (b) six in-water sections. Results are presented as $\bar{x} \pm$ SE; N = 5 days examined for tourist abundances each 2 hours between sunrise (06:00) and near sunset (18:00). See map (Fig. 1) and text for details.

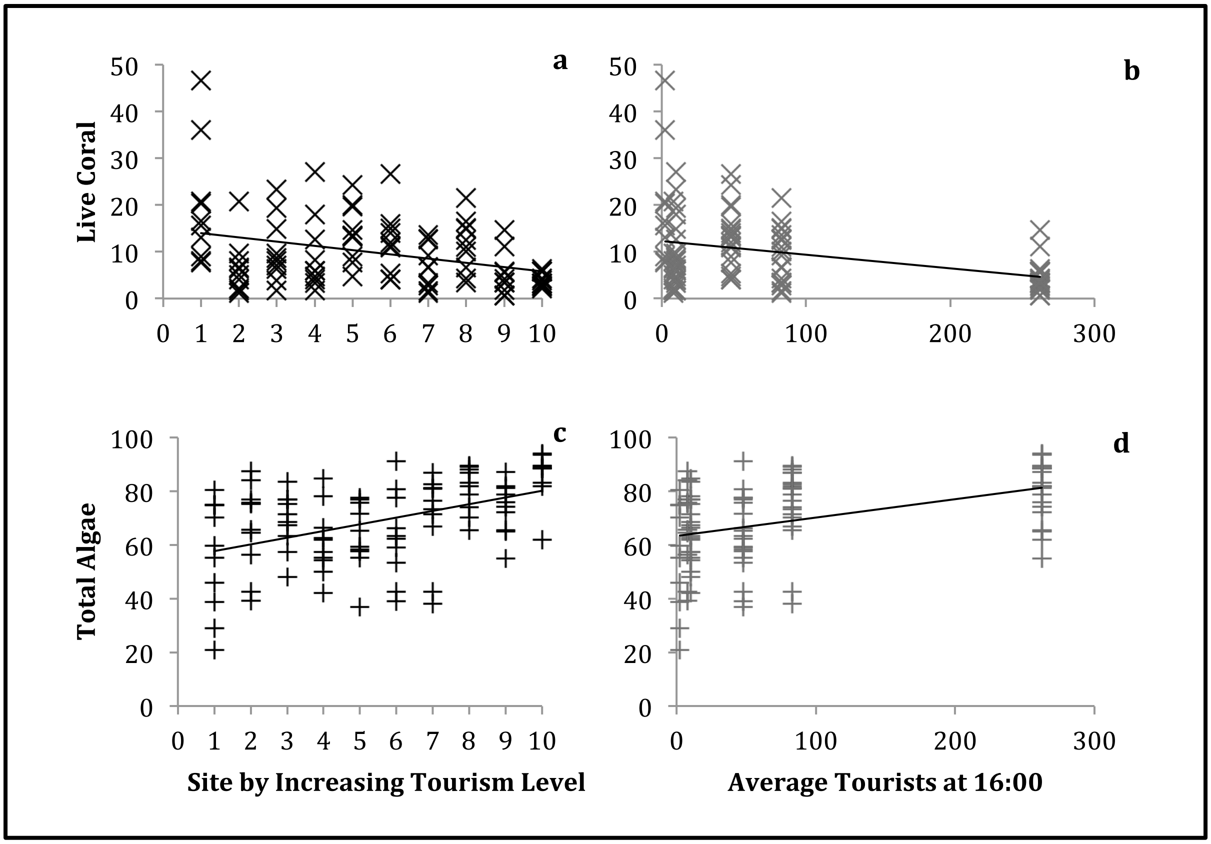

Figure 2.3. Total live coral percent cover and total algae percent cover graphed against site ranked by tourism level (a/c), and against the average number of tourists in each in-water bay section (b/d). Paired graphs show that benthic cover graphed against ranked levels of tourism and tourist abundances reveal the same patterns. Ranks will be used from here on out for easier visualization of the data.

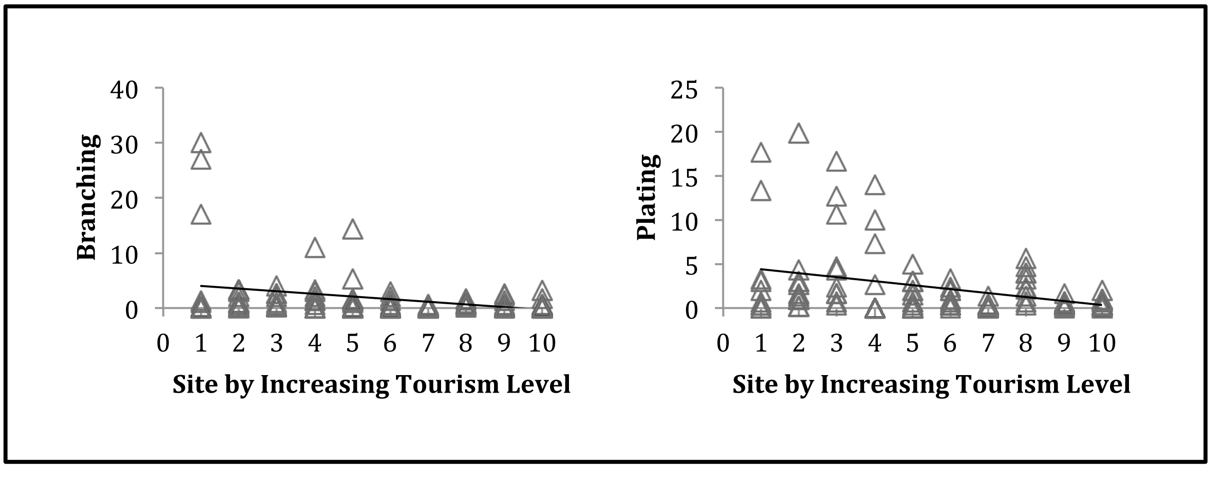

Figure 2.4. Percent cover of branching and plating coral morphological groups graphed against sites ranked by increasing tourism level.

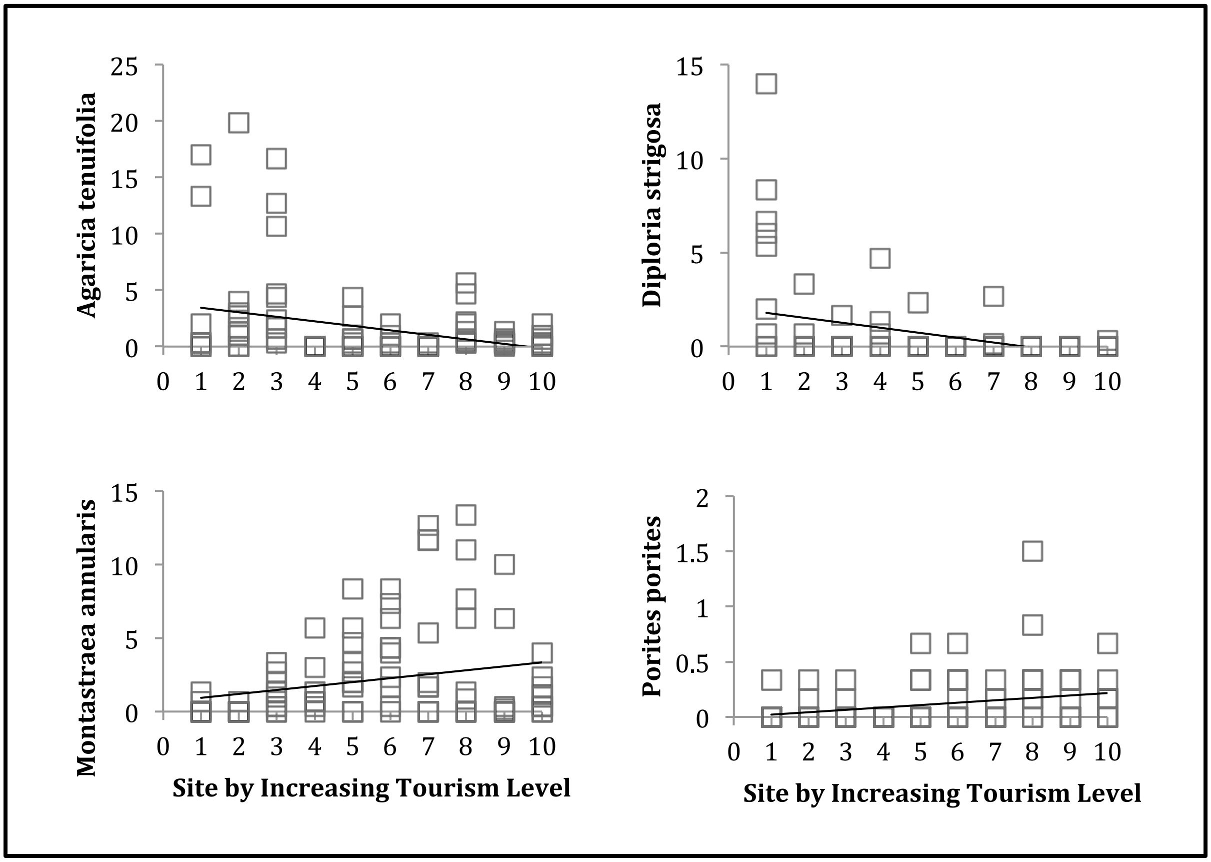

Figure 2.5. Percent cover of hard corals by species graphed against sites ranked by increasing tourism level.

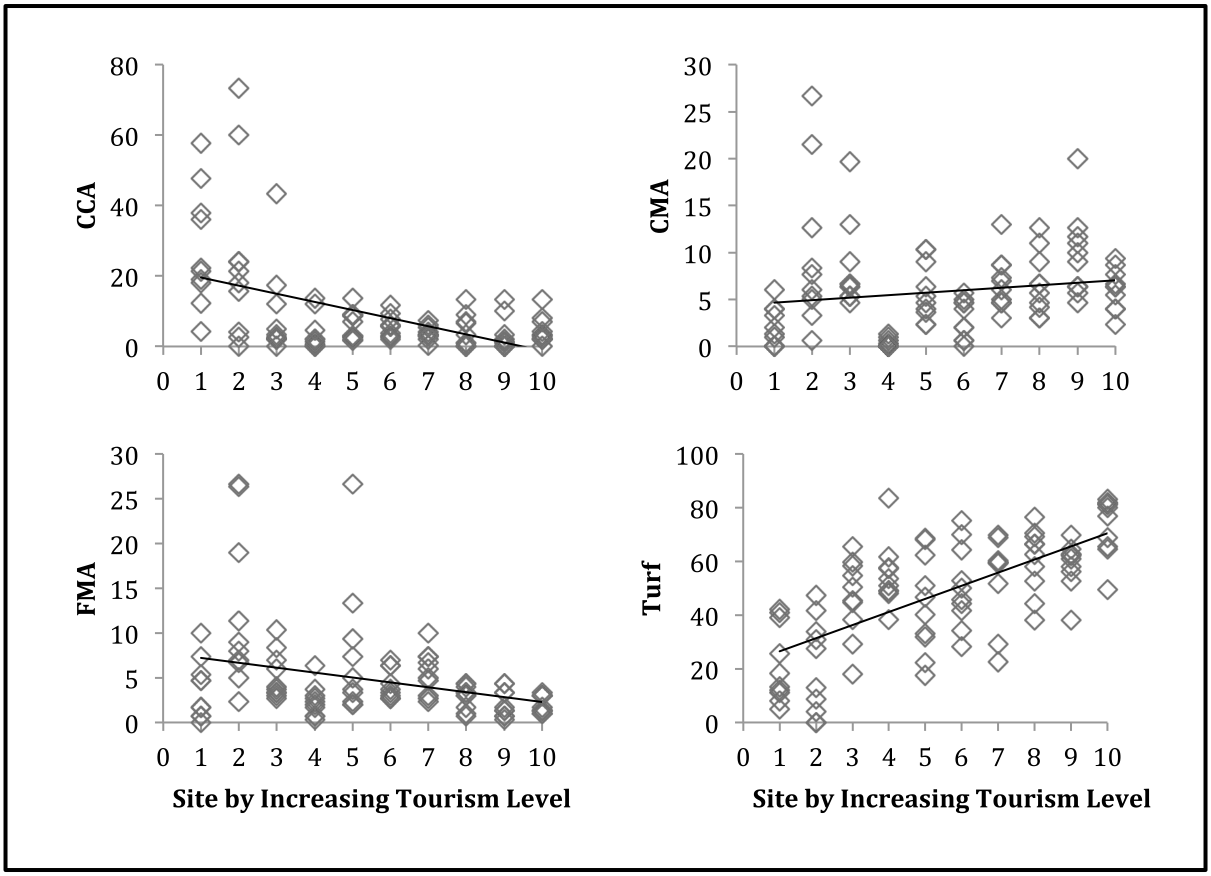

Figure 2.6. Percent cover of algae grouped by type graphed against sites ranked by increasing tourism level. Abbreviations: Crustose Coralline Algae (CCA), Calcified Macroalgae (CMA), Fleshy Macroalgae (FMA).

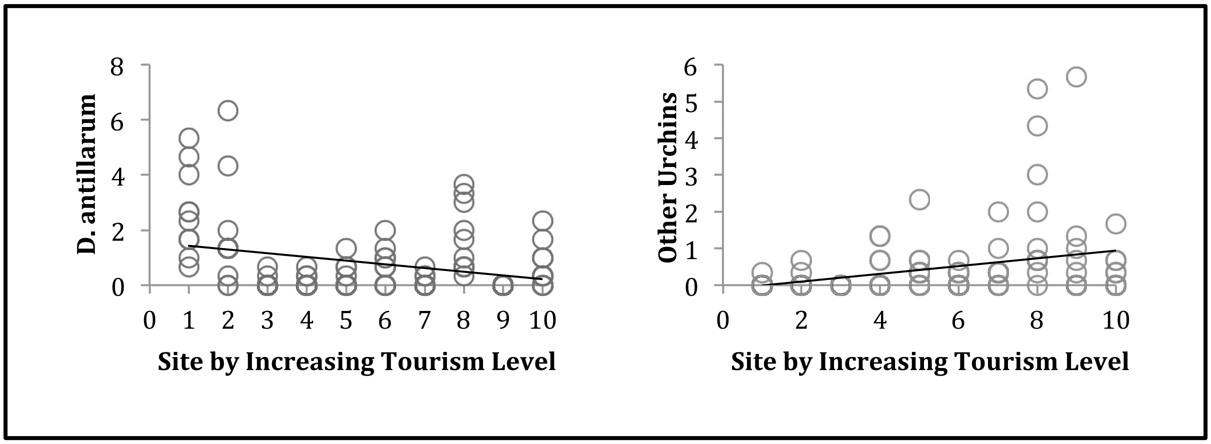

Figure 2.7. Abundance of Diadema antillarum and other urchin species graphed against sites ranked by increasing tourism level. Other urchin species category is comprised of *Arbacia punctulata* and *Eucidaris tribuloides.*

Chapter 3

Can we swim with the fishes?

Impacts of snorkeling and diving ecotourists on the foraging behavior of herbivorous reef fishes

Abstract

Fear of predation causes behavioral changes that can incur energetic costs in foraging organisms. Humans are coming into ever-increasing contact with the natural world, yet foraging models do not directly address potential costs to organisms due to interactions with humans. Ecotourists visiting coral reefs do not necessarily function as predators by hunting or intentionally acting in a threatening manner. Nonetheless, our presence has the potential to disrupt foraging behavior by herbivores in these systems based on the ecology of fear, in which the fear of possible predation can alter herbivore behavior when humans are perceived as predators. Coral reefs are an ideal model system for examining anthropogenic effects on herbivory, due to the ecological importance and ease of observation of herbivorous coral reef fishes, coupled with the increasingly-frequent exposure of these fishes to human presence. This study examines both short- and long-term effects of snorkeling and diving tourists on the behavior of herbivorous coral

reef fishes in Akumal, Mexico. Neither the abundance nor diurnal foraging patterns of the major herbivorous fishes (surgeonfishes and parrotfishes) varied significantly with tourist abundance in the water, suggesting a lack of long-term changes to the diurnal behavior patterns and habitat use of macroalgal-foraging fishes. However, they exhibited significant short-term responses to the experimentally-manipulated presence of divers. Prior to the entrance of an experimental diver to a delineated study area on the reef (5 x 3 m area), surgeonfishes and parrotfishes within this area mostly swam normally, foraged or engaged in social behaviors. After the diver entered the area, these fishes significantly altered their behaviors by rapidly escaping into open water or hiding within the reef, and decreasing their normal swimming, foraging or social behaviors. Following departure of the diver, the fishes returned within 5 min to their normal swimming, foraging and social interactions, at the same rates as pre-experiment levels. Behavioral responses of herbivorous coral reef fishes to the presence of a diver thus were similar to their known immediate responses to predators. I conclude that coral reef areas exposed to intensive diving tourism may experience frequent short-term disturbance of macroalgal foraging by herbivorous fishes, leading potentially to cascade effects that alter the structure of the coral reef community. This process could contribute to shifting coral reefs away from dominance by reef-building corals toward macroalgal dominance, similar to reefs where herbivory has been reduced by overfishing. I recommend the implementation of diver carrying capacities, coupled with targeted pre-dive education and in-water surveillance by dive guides, on coral reefs that are exposed to intensive ecotourism. These practices would reduce behavioral disturbances to the foraging of fishes that control reef macroalgae, thereby potentially enhancing the ability of reefs to resist phase shifts away from dominance by reef-building corals.

Introduction

Fear of predation causes behavioral changes that can incur energetic costs in foraging organisms (Brown 1988). Grazers as diverse as manatees and white-tailed deer are expected to remain in a foraging patch only until the costs of time spent in the patch and travel time to the next patch outweigh the gains per unit time (Nordell and Valone 2013). Brown (1988) expanded earlier optimal foraging models by defining an optimal patch model with multiple costs (OPM) that predicts the amount of time an organism will remain in a foraging patch based not only on available nutrients in the patch and travel time to the next patch, but also on additional costs such as potential predation risk in a patch, or the loss of mating opportunities due to time spent in the foraging patch (Brown 1988; Nordell and Valone 2013). For example, for desert rodents presented with 2 equal-sized piles of grain "patches", which are either covered by a bush or in the open, the covered patch is expected to be the optimal patch to forage, because it reduces the risk of being detected by predators while foraging (Brown 1988).

Foraging models like the OPM do not directly address potential costs to organisms due to interactions with humans. When humans visit ecosystems such as coral reefs or tropical forests as ecotourists, their presence has the potential to disrupt foraging behavior by the herbivores in these systems. Chronic human disruption of herbivory can lead to changes in ecosystems, because herbivores often are critical ecosystem engineers who control trophic interactions and plant abundances (Wilby et al. 2001; Harris et al. 2014). It remains unclear to what extent the herbivores alter their foraging behaviors when they detect and possibly avoid the presence of humans. Of special concern is how these effects translate into community-wide changes. Herbivores may experience increases in foraging costs if they avoid humans as perceived predators. Alternatively, they may perceive humans as benign entities to be ignored, food sources to be approached, or as filling other possible roles. Determination of the costs of human presence to foraging herbivores is increasingly critical as anthropogenic stressors to ecosystems continue to rise (Taylor and Knight 2003; Reed and Merenlender 2008). This type of information can provide a scientific basis for sustainable management strategies that aim to reduce the negative impacts of recreational activities, especially along tropical coastlines where ecotourism is prevalent (Torres and Momsen 2005; Honey 2008).

Coral reefs are an ideal model system for examining anthropogenic effects on herbivory, due to their ecological importance and ease of observation of herbivorous coral reef fishes, coupled with the increase in exposure of these fishes to human presence. Herbivorous fishes consume 50-100% of the primary production on reefs, through their consumption of filamentous and macroalgae from the surface of the reef, and their excavation of endolithic algae from within coral rock (DeLoach 1999). These fishes act as ecosystem engineers by limiting the growth of filamentous and macroalgae, so that they do not outcompete reef-building corals (DeLoach 1999). When herbivory is severely reduced, reefs may transition to an alternate stable state comprised of dominant macroalgae on coral rubble (Hughes 1994; McCook 2001; McManus and Polsenberg 2004). Healthy coral reefs support the highest biodiversity of any marine system, and are in dire need of conservation efforts due to their current rapid decline and economic importance in many countries (US Department of Commerce; Sheppard et al. 2009).

The high biodiversity on tropical coral reefs attracts extensive recreational SCUBA divers and snorkelers (referred to here collectively as ‘divers’). Divers, however, may reduce biodiversity on reefs as they inadvertently abrade, break, or kick sediment onto living corals, which can eventually alter coral community structure (Hawkins et al. 1999; reviewed in Krieger and Chadwick 2013). Several studies have examined diver effects on stony corals, but little is known about diver impacts on reef fish behavior or abundance. While some studies have reported higher fish abundance inside coral reef reserves closed to tourism versus at tourist-frequented sites (Hawkins et al. 1999), others have shown no anthropogenic effects of diving tourism on fish abundance (Claudet et al. 2010). Sea bream in the Adriatic Sea alter their escape behavior in the presence of humans, apparently due to fear of spear fisherman, by escaping into open water rather than into the reef as they do in response to natural predators (Guidetti et al. 2008). Di Franco et al. (2013) examined diver impacts on fish behavior in relation to foraging, and found that the movements of divers in the Mediterranean Sea may expose small invertebrate prey that attract some omnivorous fishes. However, herbivorous fishes are unlikely to be attracted by divers due to the sessile nature of their prey (algae), which usually are securely attached to the reef, and are not made more readily available when kicked by divers. Herbivorous fishes may instead view divers as a potential predation threat that disrupts their foraging behavior. In 2014, Rizzari et al. found that the deployment of a model shark of roughly human body size significantly reduced the foraging rates of nearby herbivorous fishes on the Great Barrier Reef, Australia. If humans are perceived as predators by herbivorous fishes, foraging models predict that our presence will disrupt their foraging activities on reefs.

Most investigations of the impacts of divers on coral reefs have been observational or correlational studies (Hawkins et al. 1999; Di Franco et al. 2013). I describe here a different approach to examination of diver impacts on reef herbivores, which includes a controlled field experiment in addition to observations. I quantified diurnal patterns in the abundance of foraging herbivorous fishes (surgeonfishes and parrotfishes) across a gradient of tourism pressure on coral reefs in Akumal Bay, Mexico, to determine possible long-term alterations in fish diurnal patterns due to diver exposure. I then manipulated diver presence to assess the immediate behavioral responses of fishes foraging on the reef.

Methods

Study Site

The present study was conducted in Akumal Bay, Quintana Roo, Mexico, located approximately 105 km south of Cancun, in a region exposed to increasing levels of reef tourism (for site details see Gil et al. 2015, Chapter 2). The bay contains a backreef of coral patch reefs interspersed with sand and sea grass beds where frequencies of tourist visitation to the bay, in the form of snorkelers are known (Gil et al. 2015, Chapter 2), and a forereef of similar sized coral patches outside the reef crest visited by divers from two SCUBA dive shops located in the bay (snorkelers and SCUBA divers are collectively referred to as ‘divers’ from here on). The known rates of divers in various parts of the bay and ease of access to both snorkel and SCUBA tours make this site an ideal location for studies on impacts of divers on reef fish behavior. The field observations described here were conducted at 2 sites on each of 10 patch reefs (described below) within Akumal Bay, (8 patch reefs were in the backreef and 2 were on the reefcrest, Fig. 3.1a). Trials for the experimental manipulation described here were conducted on 3 patch reefs in the backreef (1-3 m, snorkel depth) and 4 patch reefs in the forereef (12-18 m, SCUBA depth) during May-July 2015 (Fig. 3.1b).

Focal Fish Species

Nine focal fish species were examined: 3 surgeonfishes (ocean surgeonfish *Acanthurus bahianus,* blue tang *A. coeruleus,* and doctorfish *A. chirurgus*, which are the only surgeonfish species present in the bay) plus 6 parrotfishes (stoplight *Sparisoma viride*, princess *Scarus taeniopterus*, striped *S. iseri*, redband *Sparisoma aurofrenatum*, redtail *S. chrysopterum*, and yellowtail parrotfish *S. rubripinne*). The parrotfishes examined were the most common parrotfish species in Akumal Bay (B. Figueroa-Zavala pers. comm., B. Renfro, prelim. observ.) out of 14 species occurring in the Caribbean Sea (Humann and DeLoach 2002). An additional group ‘other parrotfishes’ were recorded for individuals not belonging to the above 6 species. Members of each of the 9 focal fish species were further categorized as juvenile or terminal phase for surgeonfishes, and juvenile, initial and terminal phase for parrotfishes, based on their ontogenic changes in coloration and body size (juveniles < 10 cm total length, Humann and DeLoach 2002).

Diurnal Patterns of Herbivorous Fish Behavior

To determine whether the abundance and behaviors of these herbivorous coral reef fishes experienced long-term shifts in diurnal activity patterns when exposed to intensive regular diver presence, I conducted field observations. Twenty sites on 10 patch reefs were selected that varied in the regular abundance of diving tourists, as determined over several years in 1 previous study and the information from Chapter 2 (Gil et al. 2015 during 2011-2014, Chapter 2 during May-July 2015): 8 low-use sites on 4 patch reefs (2 inner bay reefs #3-4 and 2 outer bay reefs #1-2, < 36 divers per day), 8 moderate-use sites on 4 inner bay reefs (reefs #5-8, < 423 people in the water per day) and 4 high-use sites on 2 inner bay reefs (reefs #9-10, ~1000 people in the water per day, Fig. 3.1a). I quantified temporal and spatial variation in the abundance and behaviors of herbivorous fishes, by assessing their abundances at each of the 20, 3 x 5m sample sites during 6 survey times (every 2 hours from 6:00-18:00). I randomly selected the site to survey during each of the 20 survey days, then conducted observations on all surgeonfishes plus parrotfishes at the selected site during the first 15 min of every other daylight hr (N = 6, 15-min survey periods per site between 06:00 – 18:00). At the beginning of each observation day between 5:30-5:45, I snorkeled to the selected site and deployed small buoys to mark off a 3x5m sampling area. The first point I reached on the near-shore edge of the patch reef was selected as the sample site (sample sites on the same patch reef did not over lap; 2 sites per reef). I then positioned myself 1 m from edge of this delineated area, and floated motionless at the water surface for 5 min to allow fishes to acclimate to my presence (after Bannerot and Bohnsack 1986; Samoilys and Carlos 2000). During the acclimation period, fishes appeared to resume their original behaviors prior to site establishment. I then recorded the number of herbivorous fishes and their behavior within the rectangular area of reef (5 x 3 m), using a point-count method adapted from Hawkins et al. (1999). I categorized fish behaviors as: foraging (head down and taking bites from the substratum), normal swimming (slow, meandering swimming above the substrate), escaping (rapid swimming, straight toward open water), hiding (rapid swimming toward a reef crevice), social behavior (interacting with other fish in a school, aggression toward other fishes, or other interactive behaviors), approach (approaching a diver, only used if divers happened to enter the sample site), and other (any activity not fitting the previous categories). I repeated this 5 min acclimation period followed by 10 min of observations at the selected site, during every other hour of the day until 18:00. If diving tourists entered the area during data collection, the number of divers was recorded. Only the backreef sites (Fig 3.1a) were examined for fish abundances, due to the difficulty of reserving boats and dive guides to access the forereef sites (Fig 3.1b) for observations 6 times each day.

Diver Presence Manipulation

I conducted a field experiment to examine potential short-term shifts in herbivorous fish abundance and behavior as immediate responses to the presence of divers. I manipulated diver presence as before (control), during, and after an experimental diver swam through my study sites (described below) at each of 7 patch reefs that were selected based on similar size and depth in each of 2 reef zones: 3 inshore backreef (1-3 m below sea surface, accessed by snorkeling tourists, reefs #2, 6, and 10 in Fig. 3.1a and b) and 4 offshore forereef (10 -13 m, accessed by SCUBA diving tourists, reefs YKS, HMBS, AKS, and ESC in Fig. 3.1b). Each sample site on the 7 patch reefs was selected also based on the presence of an adjacent easily-accessible sand flat, so that the observer could remain motionless on the sand flat while recording data from a haphazardly-selected experimental site of 5 x 3 m on the neighboring patch reef, which was marked by neon flags at each corner. I then manipulated diver presence in the experimental area, according to 3 sequential treatments: before (control), during, and after a volunteer diver swam through the experimental site. The observer remained motionless on the seafloor throughout the experiment (after Hawkins et al. 1999), while the volunteer was instructed to swim through the site while exhibiting typical behaviors of diving tourists, such as taking photographs with an underwater camera, pursuing individual fish over short distances, and moving up and down as diver buoyancy changed. Prior to the start of each experiment, fishes were allowed to acclimate for 5 min after the site was flagged and the observer settled onto the sand flat (similar to the process during field observations above, after Bannerot and Bohnsack 1986; Hawkins et al. 1999). I then applied 3 treatments each for 5 min: (1) Before (control): observer recorded fish abundance and behaviors before the volunteer diver entered the site, using a point-count method same as for the field observations above (adapted from Hawkins et al. 1999; Samoilys and Carlos 2000), in a rectangular column extending up from the 5m x 3m benthic site to the surface (though fish rarely swam more that 2 - 3m above the reef), (2) During: volunteer diver was signaled to enter the site, and fish abundance and behaviors again were recorded while the volunteer swam back and forth through the site for 5 min at a rate of ~ 0.5 m/s (similar to the swimming rates of diving tourists in the bay, B. Renfro, preliminary observations) 1 - 2 m above the reef, (3) After: diver has left the site; fish abundances and behaviors again recorded for 5 min. The ‘after diver presence’ treatment was set at 5 min, because the period for fish to acclimate to a new object in their environment is < 5 min (Bannerot and Bohnsack 1986; Samoilys and Carlos 2000), and the experiment was designed to determine whether fish immediately returned to normal abundances and behaviors post-exposure. Based on preliminary observations, this was sufficient time for fish to return to the site and behave normally, so the treatment time was not extended. Each experiment thus lasted 20 min total (5 min acclimation, followed by 5 min for each of 3 treatments: before, during, and after diver presence). I categorized fish behaviors as described above (see observational study). This 20-min experiment was repeated 12x on the backreef (snorkel; 5x at patch reefs #6, 10 and 2x at patch reef #2), and 16x on the forereef (SCUBA; 5x at YKS, 4x at HMBS, 4x at AKS, and 3x at ESC). The experiment was performed at each reef 1 - 3x on a given day, and individual 5m x 3m sites at each reef were not reused (ie: the site was moved to a different location on each reef, each time).

Data Analyses

To statistically analyze diurnal patterns of foraging fish abundance, I combined sites by their tourist-use level (High: 2 sites on each of reefs #9-10, Moderate: 2 sites on each of reefs #5-8, and Low: 2 sites on each of reefs #1-4, Fig. 3.1a; after Chapter 2 tourist abundance surveys), to reveal patterns of diurnal fish foraging behavior in relation to tourism pressure. Normality was examined using Shapiro-Wilk normality test and qqplots and data were transformed where necessary. Each time period (6:00-18:00) was examined separately for differences in total fish abundance between tourism levels (High, Moderate, Low) using Analysis of Variance (ANOVA) with R version 3.1.3 (R Core Team 2015). Where significant differences across tourism levels were found, post hoc pairwise comparisons were run using Tukey's Honest Significant Difference Test. Abundance of fish exhibiting each behavior (normal swimming, foraging and social behaviors) was then analyzed separately for each time period across tourism levels. Escape, hide, approach and 'other' behaviors were omitted from analyses due to rare occurrence.

To statistically analyze changes in fish behavior between diver manipulation treatments, each behavioral category (normal swim, escape, hide, forage, social) was analyzed separately. I employed a Generalized Linear Model (GLM) assuming a Poisson distribution for count data with R version 3.1.3 (R Core Team 2015), to determine whether fish behavior varied significantly with treatment (before, during and after diver presence), diver activity type (snorkel vs SCUBA) and fish type (surgeonfishes vs parrotfishes). The Poisson regression assumption of equidispersion was verified using the dispersion test in R package AER. In cases where over dispersion was found, the model was re-fit with quasipoisson distribution to account for the data dispersion pattern. Post-hoc pairwise comparisons to determine differences in foraging fish abundance between each pair of bay sections were made using Tukey's Honest Significant Difference (HSD) test, using R function Simultaneous Tests for General Linear Hypotheses in R package multcomp. Behaviors approach and ‘other’ were removed from analyses based on extremely rare occurrence.

Results

Diurnal Patterns of Fish Behavior

The abundance of herbivorous fishes did not differ significantly among the high, moderate and low tourist-use sections of the bay (ANOVA: all $p > 0.05$) during any of the 2-hr periods examined each day (6:00 thru 18:00, Fig 3.2). The abundance of herbivorous fishes swimming normally only differed significantly between tourism levels at 8:00 (ANOVA: $F = 4.881$, $p = 0.021$, Fig 3.3a) with the moderate and low tourist-use sections of the bay containing more fish swimming normally than the high section of the bay (TukeyHSD: $p = 0.032$ and 0.026 for high vs low and high vs moderate respectively). Abundance of herbivorous fishes swimming normally did not differ between tourism levels for any other times during the day (ANOVA: all $p > 0.05$, Fig 3.3a). The abundance of herbivorous fishes foraging did not differ significantly among the high, moderate and low tourist-use sections of the bay (ANOVA: all $p > 0.05$) during any of the 2-hr periods examined each day (Fig 3.3b). The abundance of herbivorous fishes exhibiting social behaviors only differed significantly between tourism levels at 10:00 (ANOVA: $F = 4.451$, $p = 0.028$, Fig 3.3c) with the low tourist-use section of the bay containing slightly insignificant greater numbers of fish acting socially than the moderate and high use sections of the bay in pairwise comparisons (TukeyHSD: $p = 0.055$ and 0.058 for high vs low and low vs moderate respectively).

Diver Presence Manipulation

The abundance of herbivorous fishes that performed each type of behavior differed significantly among the experimental diver treatments (Before, During and After diver presence), for all major behaviors examined: normal swimming, escaping, hiding, foraging and social behaviors (GLM, Normal: $t = -6.397, -9.668, -6.666$ for Before, During, After respectively, all $p < 0.001$; Escape: $t = -8.313, -9.602, -9.860$ for Before, During, After respectively, all $p < 0.001$; Hide; $t = -10.518, -12.369, -9.476$ for Before, During, After respectively, all $p < 0.001$; Forage: $t = -6.653, -9.547, -7.149$ for Before, During, After respectively, all $p < 0.001$; Social: $t = -7.946, -6.916, -7.811$ for Before, During, After respectively, all $p < 0.001$).

In post hoc pairwise comparisons, the ‘before’ (control) and ‘after’ diver treatments did not differ significantly, while both differed significantly from the during-diver treatment, for all behaviors (Table 3.1). Thus, significantly more fish swam normally, foraged and engaged in social behaviors both before and after diver presence, than during diver presence in the study plots (Table 3.1, Fig. 3.4). In contrast, significantly more fish exhibited escape or hide behaviors during diver presence, than before or after diver presence in the same areas (Table 3.1, Fig. 3.4).

Significantly different numbers of fish exhibited normal swim, hide, forage and social behaviors (Fig. 3.4), but not escape behavior, in response to the 2 examined types of recreational activity by divers (SCUBA diving vs. snorkeling). Significantly more fish exhibited normal swimming and social behaviors when exposed to divers on SCUBA than on snorkel (GLM: $t = -5.312, -3.623$ for normal swim and social respectively, $p < 0.001$, Fig 3.4). A slightly but significantly greater number of fish exhibited hiding behavior when approached by divers on snorkel compared to SCUBA (GLM: $t = 2.115$, $p = 0.0345$, Fig 3.4). Also, significantly more fish foraged during the snorkel trials compared to SCUBA trials (GLM: $t = 6.493$, $p < 0.001$). However, while the abundances of fish exhibiting each behavior differed between SCUBA and snorkel trials, the patterns between treatments held the same for both activity types.

Significantly more parrotfish than surgeonfish exhibited normal swim, escape, hide, and forage behaviors, but not social behaviors during diver presence treatments (GLM: $t = 3.344, 2.060, 4.164, 2.961$ for normal swimming, escaping, hiding, foraging respectively; $p < 0.001$ for normal swimming and hiding, $p = 0.0395$ and 0.0031 for escaping and foraging respectively). While more parrotfish exhibited each of these behaviors the proportions (Fig 3.5) of parrotfish per behavior and surgeonfish per behavior were the same. The patterns between treatments held the same for both fish families.

Discussion

Herbivores are critical ecosystem engineers (Wilby et al. 2001; Harris et al. 2014), especially on coral reefs where they maintain the balance between competing stony corals and macroalgae (Mumby 2006b). Foraging models have explored several potential costs and benefits influencing herbivore patch preference, but have yet to include the potentially unique effects of non-consumptive human disturbance on herbivore behavior (Brown 1988; Nordell and Valone 2013). The present study revealed that fishes responded to divers similarly to how they would be expected to respond to a predatory threat, by departing from the foraging patch. Fear of human presence as potential predators was sufficient to alter fish behavior, as predicted by the ecology of fear, in that predator presence affects prey foraging behavior and thus primary producer abundance, separately from the impacts of direct consumption of prey (Brown et al. 1999; Cherry et al. 2016). The results here indicate that the presence of humans near wild animals should be considered similarly to predator presence under foraging models, even if they do not partake in hunting activity.

The ‘landscape of fear’ concept in fear ecology explains how organisms behave in and move about their environments, based on the level of perceived risk across the landscape, or in the present case ‘seascape’ (Brown et al. 1999; Laundré et al. 2010). However, the seascape of fear does not influence all marine prey species; loggerhead turtles do not alter their behavior or habitat use when passing between areas of more or less tiger shark predation risk (Hammerschlag et al. 2015), similar to the results here in which long-term differences in herbivorous fish diurnal behavior patterns in Akumal Bay were not observed between areas of high, moderate and low tourism. One explanation may be that the parrotfishes and surgeonfishes in the high tourism section of Akumal Bay may be partially habituated to tourist presence, as observed for the client fishes who visit cleaning stations on heavily-dived reefs in Honduras (Titus et al. 2015). However, my experimental results demonstrate that fear responses drive immediate, short-term changes in the abundance and behavior of herbivorous fishes when in the direct presence of a diver even if this fear does not extend to changes in overall habitat use it still disrupts foraging behavior.

If fishes are able to only partially habituate to diver presence (Titus et al. 2015), then the critical role of parrotfishes and surgeonfishes as herbivores on reefs will continue to be interrupted by short-term responses to diver presence. On reefs that are infrequently-dived, these immediate short-term changes in herbivore behavior may not result in substantial changes to the trophic cascade that affects benthic community structure. However, on reefs which experience heavy tourist use, such as portions of Akumal Bay (Chapter 2), continuous contact with humans throughout the day could trap herbivorous fish in a continual cycle of reactions to short-term disturbances, ultimately preventing these fish from adequately consuming reef algae. This could result in major energetic costs to the fish (lack of foraging opportunity, energy spent escaping, Brown 1988) and also loss of herbivory on reef algae, which is correlated with phase shifts in the reef structure from stony coral to macroalgal dominance (McCook 2001; McManus and Polsenberg 2004; Durán and Claro 2009).

In order for diving tourism on coral reefs to be a sustainable industry, time must be allotted each day for herbivorous fish to forage undisturbed on reefs. For offshore reefs, this can be easily managed by limiting the number of dive tours that visit a particular reef per day, and possibly their timing during the day, allowing the reef to be free of any diver presence for part of the day. For inshore reefs, however, the task may prove more difficult. At Akumal Bay, snorkelers are allowed to enter the water from shore with or without a guide. For some reefs such as those at Akumal, diver education may be a partial solution to the problem of excessive disturbance of normal fish behaviors. Public signage and tour guide instruction can be used to educate visitors on the importance of remaining a minimum distance from fishes as well as from the reef surface, in order to inflict as little damage as possible while exploring this fragile ecosystem. Education, however, may not be enough; in Akumal, for example, illegal tour groups from other towns have removed or destroyed educational signs in town and on the beach. For reefs like this, governmental regulation of the number of snorkelers or snorkel tours permitted access to the bay on a daily basis may be required. In these instances, cooperation with local stakeholders and access to the reef for citizens of the local town would be necessary to keep with the concept of ecotourism, which is meant, by definition, to benefit not only the environment but the local culture, as well.

Tables and Figures

Table 3.1. Simultaneous Tests for General Linear Hypotheses results. Z statistic values and P-values for post-hoc pairwise comparisons of the number of fish exhibiting each type of behavior during each of 3 experimental field treatments (Before, During and After diver presence; see text for details).

	Treatment	Before	During
Normal Swimming	During	Z = -5.406 P < 0.001	--
	After	Z = 0.320 P = 0.944	Z = -5.159 P < 0.001
Escape	During	Z = 5.697 P < 0.001	--
	After	Z = -1.005 P = 0.561	Z = 6.233 P < 0.001
Hide	During	Z = 4.590 P < 0.001	--
	After	Z = 0.532 P = 0.85	Z = 4.471 P < 0.001
Forage	During	Z = -4.235 P < 0.001	--
	After	Z = 0.656 P = 0.791	Z = -3.640 P < 0.001
Social Behaviors	During	Z = -2.428 P = 0.038	--
	After	Z = -0.773 P = 0.713	Z = -2.965 P = 0.0078

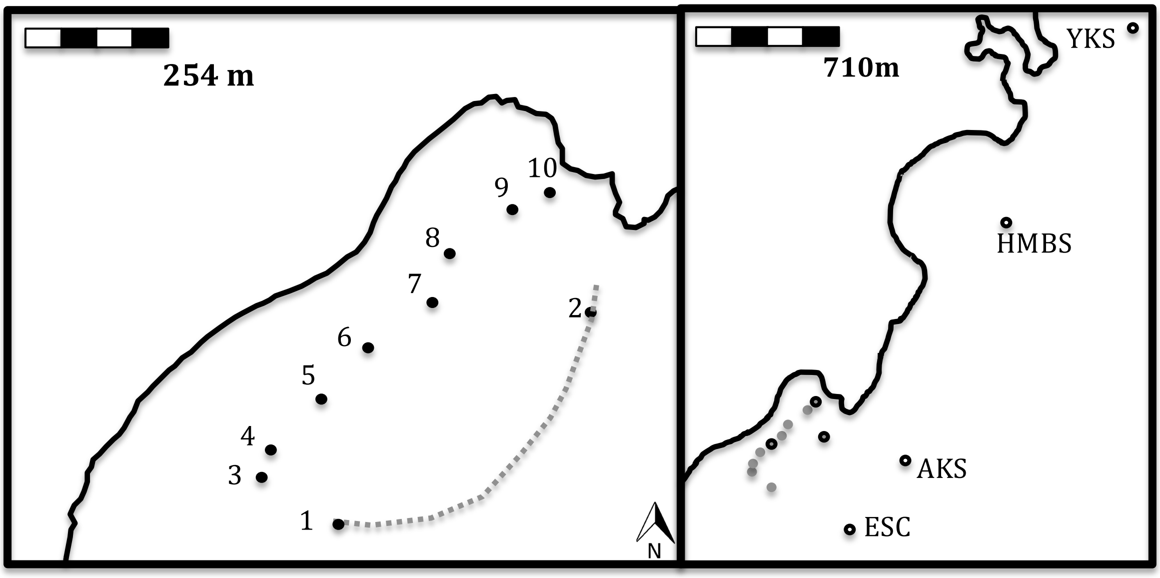

Figure 3.1a (left): Map of Akumal Bay. Numbers indicate study reefs for benthic and fish surveys. Tourist count data showed #9-10 experience high tourism, #5-8 experience moderate tourism, #1-4 experience low tourism. Grey dotted line denotes the reef crest. **1b (right):** Sites used for experimental trials. Trials on snorkel ran at sites #2, 6, 10 in the Akumal Bay, 1-3m depth. Trials on SCUBA run at Yal Ku Somero (YKS), Half Moon Bay Somero (HMBS), Akumal Somero (AKS), and La Escuelita (ESC), 12-18m depth.

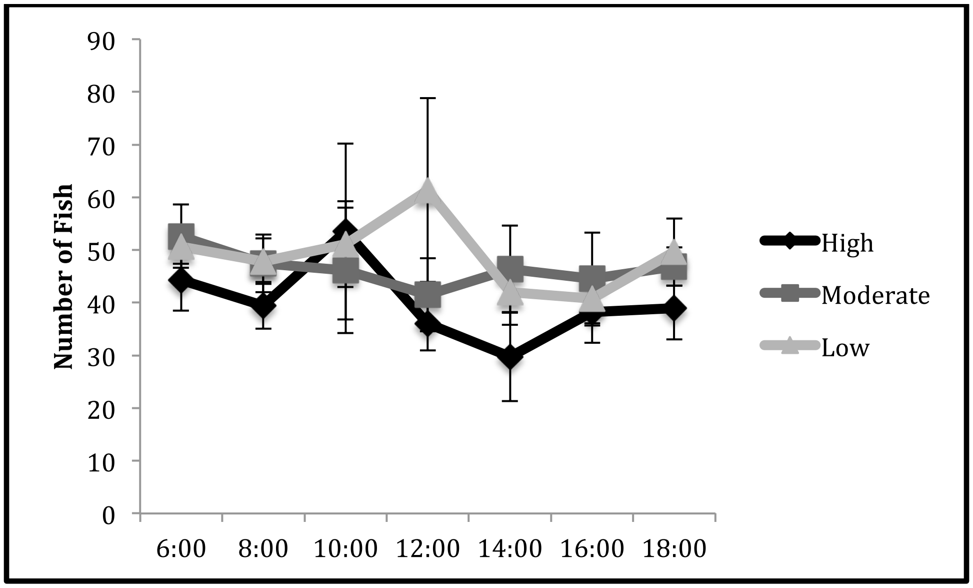

Figure 3.2. Variation in the abundance of herbivorous fishes with time throughout the day and level of diving tourism (high, medium, low) on coral reefs in Akumal Bay, Mexico. Results are presented as $\bar{x} \pm$ SE; N = 4 sites on 2 patch reefs in high tourism and 8 sites on 4 patch reefs in moderate and low tourism. See Fig. 1 and text for details.

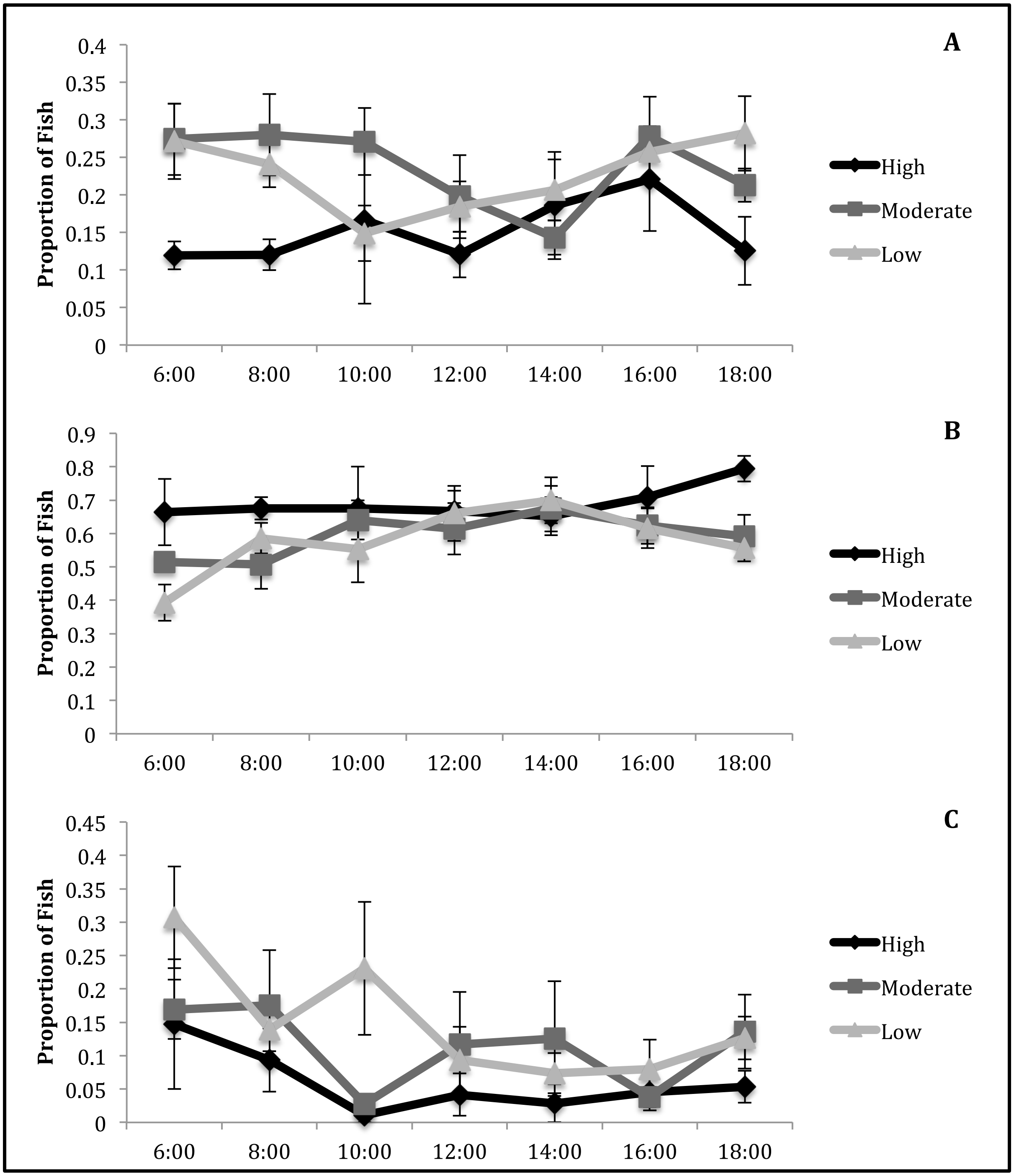

Figure 3.3a, b and c. Variation in the proportion of herbivorous fishes (a) swimming normally, (b) foraging and (c) exhibiting social behaviors with time throughout the day and level of diving tourism (high, medium, low) on coral reefs in Akumal Bay, Mexico. Results are presented as $\bar{x} \pm$ SE; N = 4 sites on 2 patch reefs in high tourism and 8 sites on 4 patch reefs in moderate and low tourism. See Fig. 1a and text for details.

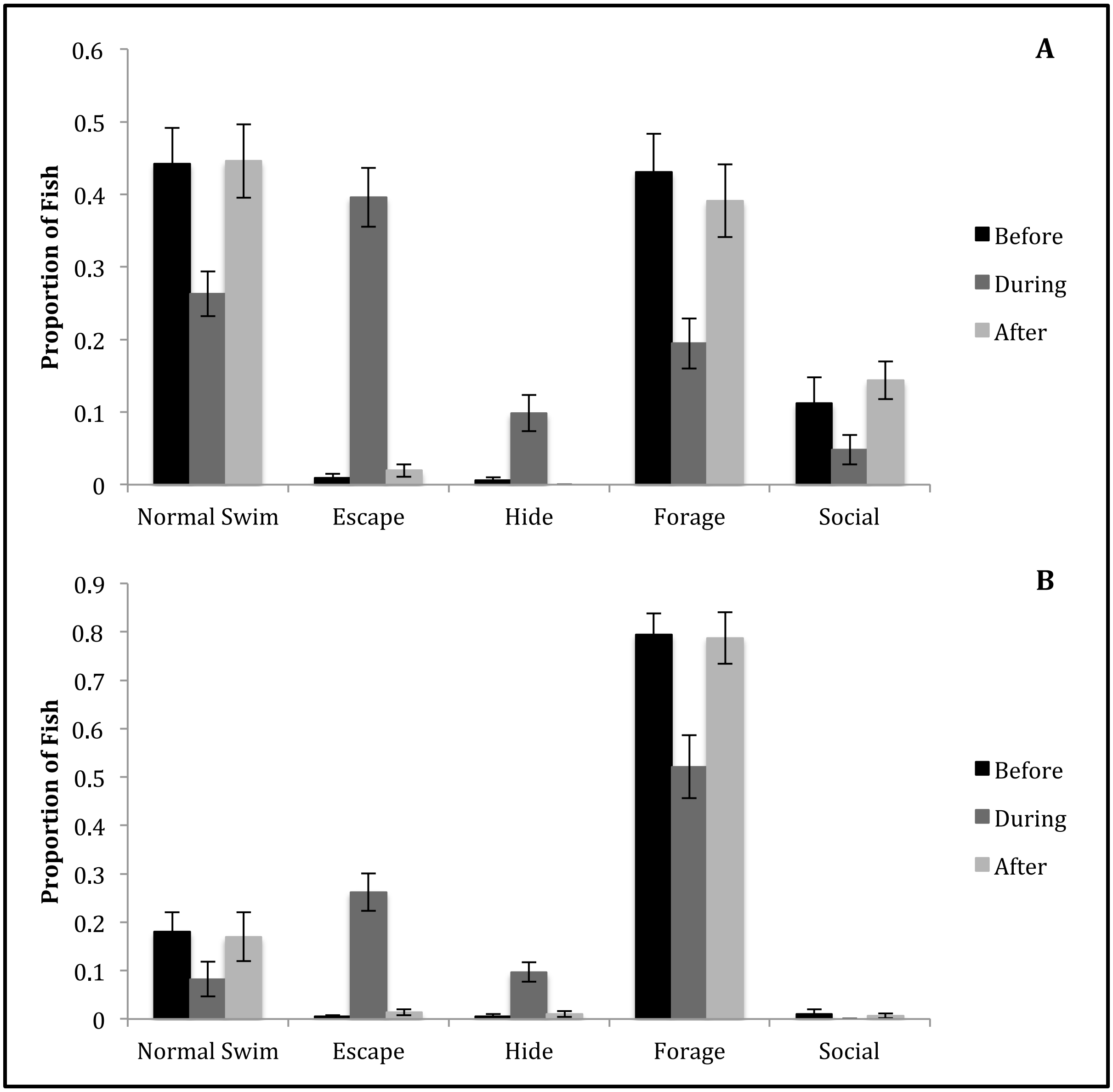

Figure 3.4. Variation in the numbers of herbivorous fishes exhibiting 5 types of behaviors in response to experimental manipulation of the presence of 2 types of divers: (a) SCUBA (N = 16 trials), (b) snorkel (N = 12 trials). Results are presented as $\bar{x} \pm$ SE. Before, During, and After represent the 3 types of treatments applied in each experiment, in terms of diver presence in the experimental sites, Before=control. See text for details.

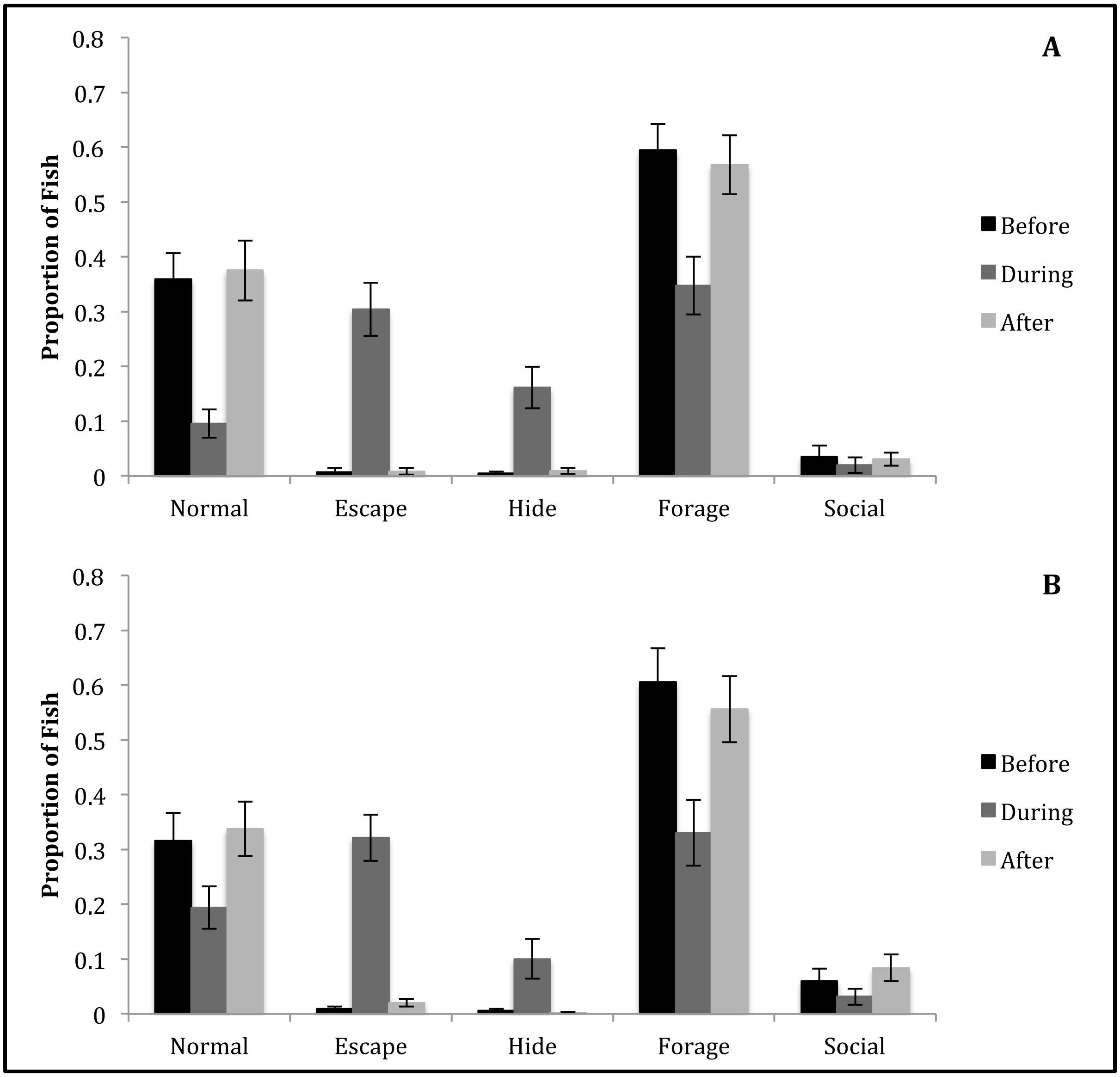

Figure 3.5. Variation in the numbers of herbivorous (a) surgeonfishes and (b) parrotfishes exhibiting 5 types of behaviors in response to experimental manipulation of the presence of a diver. Results are presented as $\bar{x} \pm$ SE. Before, During, and After represent the 3 types of treatments applied in each experiment, in terms of diver presence in the experimental sites, before=control. See text for details.

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