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BOAT ANCHORING CONTRIBUTES TO CORAL REEF DEGRADATION IN THE BRITISH VIRGIN ISLANDS

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BOAT ANCHORING CONTRIBUTES TO CORAL REEF DEGRADATION IN THE BRITISH VIRGIN ISLANDS

BY

REBECCA LOBERG FLYNN

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2015

MASTER OF SCIENCE THESIS

OF

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APPROVED:

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UNIVERSITY OF RHODE ISLAND
2015

Abstract

Habitat degradation is occurring the world over, threatening species, population dynamics, ecosystem function and valuable ecosystem services. This degradation is in many cases linked to anthropogenic activities, which often reduce a habitat's resilience to other stressors. Coral reef decline, for example, has been linked to climate change, pollution, and overfishing. Few studies have focused on the local-scale physical drivers of coral decline, such as anchoring. As global human population and the popularity of water-based recreation continue to rise, the potential for anchoring to contribute to coastal habitat degradation increases. We sought to determine the potential impact of anchoring to coral reefs by conducting a spatial survey of sites that represent a gradient of anchoring activity in the British Virgin Islands. We collected data on benthic community composition, coral colony size and density, species richness and abundance. We also evaluated reef rugosity and fish population densities. Cover of hard corals and sea fans were both reduced by ~7% at highly anchored sites. Hard corals were ~40% smaller in size and ~60% less dense at sites experiencing high anchoring frequency. In addition, highly anchored sites supported only ~60% of the species richness of little anchored sites. Finally, frequently anchored sites were ~60% as structurally complex and supported only 45% of the fish density as those rarely anchored, with some fish functional groups more affected than others. Anchoring is a major driver of reef community decline, but it is also a relatively tractable management issue. Knowing how local, physical anthropogenic stressors contribute to reef decline can inform management that will promote reef resilience, ecological function, and ecosystem services.

Acknowledgements

I am incredibly grateful for the assistance and guidance my advisor, Graham Forrester, has provided at every stage of this project from brainstorming through planning and data collection to writing and dissemination of results. I have been aided greatly by the rest of my committee (Lianna Jarecki, Jason Kolbe, and Gavino Puggioni) in planning, locating sites, and analyzing my data. I appreciate the field assistance of Jessica Perreault, David Gleeson, and Kristian Dzilenski; without them, I would not have been able to collect as much data. This work would not have been possible without the funding provided by The Falconwood Foundation and The Nature Conservancy's Global Marine Team. Finally, deepest thanks to the Guana Island staff, Dive BVI, and UBS Divers for their logistical support.

Dedication

I hereby dedicate this thesis to all the people who have supported, loved, and encouraged me throughout the years. I especially dedicate this to my parents, Charlotte and Michael Flynn, for teaching me to value the good things in this world and showing me the true meaning of success. I cannot express how much their faith in me and their unconditional love have meant. I have also been blessed with supportive incredible siblings, who, through their pursuit of their own ambitions, inspired and challenged me to seek a field about which I can truly be passionate. To all the friends, roommates and companions on this journey who have seen me through both the good times and the hard ones, I express my unending gratitude. Additional thanks to my family and friends, as well as many of my teachers, mentors, and coworkers ignited and fanned the spark of my passion for science, specifically environmental studies, conservation biology, and coastal marine ecosystems. Finally, I dedicate this to David, who shared in my joys and my struggles and brightened my days. I have been truly blessed by all the people in my life who have helped me to this point. Nothing is ever accomplished alone, so this accomplishment is as much yours as it is mine.

Preface

The following thesis is in manuscript format. It contains one manuscript, which follows the guidelines for publication in the journal Ecological Applications. This research is being prepared for submission to Ecological Applications, but at the time of defense, has not yet been submitted.

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Manuscript

Boat Anchoring Contributes to Coral Reef Degradation in the British Virgin Islands

Rebecca L. Flynn[1] and Graham E. Forrester[1]

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In preparation for submission to Ecological Applications

Abstract

Habitat degradation is occurring the world over, threatening species, population dynamics, ecosystem function and valuable ecosystem services. This degradation is in many cases linked to anthropogenic activities, which often reduce a habitat's resilience to other stressors. Coral reef decline, for example, has been linked to climate change, pollution, and overfishing. Few studies have focused on the local-scale physical drivers of coral decline, such as anchoring. As global human population and the popularity of water-based recreation continue to rise, the potential for anchoring to contribute to coastal habitat degradation increases. We sought to determine the potential impact of anchoring to coral reefs by conducting a spatial survey of sites that represent a gradient of anchoring activity in the British Virgin Islands. We collected data on benthic community composition, coral colony size and density, species richness and abundance. We also evaluated reef rugosity and fish population densities. Cover of hard corals and sea fans were both reduced by ~7% at highly anchored sites. Hard corals were ~40% smaller in size and ~60% less dense at sites experiencing high anchoring frequency. In addition, highly anchored sites supported only ~60% of the species richness of little anchored sites. Finally, frequently anchored sites were ~60% as structurally complex and supported only 45% of the fish density as those rarely anchored, with some fish functional groups more affected than others. Anchoring is a major driver of reef community decline, but it is also a relatively tractable management issue. Knowing how local, physical anthropogenic stressors contribute to reef decline can inform management that will promote reef resilience, ecological function, and ecosystem services.

Key words: coral reef, stressor, boat, recreation, marine tourism, habitat decline, anchor, anthropogenic

Introduction

Human activities are degrading habitats on a global scale, resulting in a loss of biodiversity, trophic collapse, and diminished ecosystem function and services (Ehrlich and Wilson 1991, Naeem et al. 1994, Dobson et al. 2006). Coral reefs, in particular, are high diversity habitats accounting for approximately one quarter of the ocean's biodiversity while occupying less than 0.01% of the marine environment (Burke et al. 2011). Reefs perform several ecosystem services by protecting shorelines, supplying fisheries, and attracting tourism and recreation that provide nations with revenue (Burke et al. 2011). Coral reefs are, however, declining globally (Gardner et al. 2003; Schutte et al. 2010) and losing three-dimensional complexity (Alvarez-Filip et al. 2009). Both diminishing coral cover and complexity negatively impact reef fish, some of which rely on live coral for food while others utilize the structure as refuge (Lewis 1998; Graham et al. 2009).

Reef degradation is caused by the integrative effects of natural disturbances, such as hurricanes, and anthropogenic stressors (Wilkinson and Buddemeier 1994; Wilkinson 2008). Key anthropogenic stressors include global climate change (ocean warming and acidification) and local effects from overfishing, coastal pollution, invasive species, and "too many people," including those engaged in marine recreation (Wilkinson 2008; Jackson et al. 2014).

Anchoring is one symptom of “too many people,” (Jackson et al. 2014) that may contribute to reef degradation. As ocean recreation and the associated boat traffic increase rapidly in many areas of the world (Davenport and Davenport 2006; Burgin and Hardiman 2011), physical damage to reefs may also increase. Physical damage from boat anchors and the associated chains (hereafter, collectively referred to as anchors or anchoring) is an acknowledged source of damage to coral reefs (Goenaga 1991). Compared to other human impacts, however, boat anchoring has been the subject of virtually no formal study (Johnstone et al. 1998). By way of illustration, a search of Web of Science for “coral reef anchor” returns only 68 papers, whereas a search for “coral reef climate” returns 2,335 and one for “coral reef fishing” returns 6,234. The mechanisms by which anchors damage reefs have been detailed, such as dislodging (McManus et al. 1997), overturning (Glynn 1994; Dinsdale and Harriott 2004), and crushing corals (Fava et al. 2009). Researchers have considered possible metrics for anchor damage (Dinsdale and Harriott 2004). However, the few estimates of coral cover loss due to anchoring are highly variable (between 0.3%/year and 7%/year (McManus et al. 1997; Saphier and Hoffmann 2004)) and may be based on unrealistic assumptions. Edinger et al. (1998) found that the coral species richness of a reef subject to both anchor damage and pollution was 50% and 10% lower at 3 m and 10 m depths, respectively, than sites unaffected by human activities. Anchoring may impact organisms other than corals since the crushing of corals can contribute to reef flattening and loss of refugia (Fava et al. 2009). For instance, some species of coral-associated fishes disappeared from experimentally damaged reef patches in the Great Barrier Reef (Lewis 1998). In addition, anchor damage could contribute to shifts in community assemblage. Anthropogenically disturbed reefs have diminished resilience and often shift to communities dominated by non-coral taxa, such as macroalgae (Carilli et al. 2009, Dudgeon et al. 2010, Rogers and Garrison 2001, Schlöder et al. 2013, Maynard et al. 2010).

Although informative, previous studies do not address the community-wide impacts from chronic anchor damage. The dearth of information on how anchoring impacts community structure and function highlights the value of an ecosystem-wide study. Our objective is to document the quantitative effects of chronic anchor damage to coral reefs through a rigorous comparison of anchor-damaged and undamaged reefs and assessment of both the direct impacts on sessile species like corals and sea fans, and the indirect effects on reef-associated fishes. We expected that reefs that have experienced higher anchoring activity would support fewer and smaller corals and sea fans. Consequently, we also expected anchor-damaged reefs would lose structural complexity and so have lower densities of reef-associated fishes. In principle, mitigating the effects of physical anchor damage should represent a more tractable management problem than many global stressors, such as ocean warming. Local management of boat anchoring should promote reef resilience, while at the same time allowing continued tourism and recreation. Quantifying the contribution of anchoring to coral reef decline should help inform the design of best management practices for anchoring near coral reef habitat.

Methods

Study Location

We studied the effects of anchoring on reefs in the British Virgin Islands (BVI) because the number of active vessels and their size contribute to a high risk of anchor damage to reef habitats in this territory. Approximately 1100-1500 yachts (12-16 m in length) operate in the 155 km^2 of BVI water (personal communication with Janet Oliver, BVI Charter Yacht Society, and Trish Baily, BVI Association of Reef Keepers and BVI ReefCheck). This fleet is expanding and visitation by larger mega-yachts (exceeding 45 m in length) is increasing. Few restrictions on anchoring within coral reefs exist in the BVI, and those that do have never been enforced (personal communication, Lianna Jarecki, Guana Science, BVI).

Site Selection

During the summer of 2014, we surveyed 25 reefs in the BVI to determine the effects of chronic anchoring. Sites along a gradient of anchoring activity were selected and categorized as experiencing low (little or no) (n =11), medium (n = 4) or high (n = 10) anchoring (Fig. 1). Classification was based on the plausibility of use as an anchorage, expert opinion, the observed density of yachts, and the presence of symptoms of anchor damage. Plausible anchorages are situated on the leeward sides of islands, usually near sand, and often in bays. Expert opinion about the level of anchoring at potential study sites was obtained by consulting with local professionals, such as dive instructors and charter captains. We selected sites for which there was consensus about the extent of anchoring. In addition, we verified our classifications by examining historical imagery on GoogleEarth, which dated from 2004-2014, and counting boats anchored at each site (Fig. 2). We assessed all available images that were not obscured by clouds (between 4 and 10 images per site). Since we knew the locations of most moorings, we could exclude moored boats from these counts. Low anchoring sites, which represent controls, were geographically close to anchor damaged sites and were similar in characteristics such as depth, wave exposure, and reef slope, but were infrequently anchored based on expert opinion and lack of damage symptoms. A group variable was used to account for other sources of variation. Each site was assigned to a group based on geographic proximity and similarity in physical variables such as depth, wave exposure and reef slope. All groups included at least one high and one low anchoring site.

To assess the possibility of land-use influences on reef communities, we used the ruler tool in GoogleEarth to measure the distance from each site to the nearest shore and the nearest developed land area (Lirman and Fong 2007) (Fig. 3). Finally, to determine what percentage of reef in the BVI is potentially vulnerable to anchoring we used GIS to classify coral reefs by exposure (leeward or windward), based on the assumption that only leeward reefs are potential anchoring sites. The GIS feature class utilized was a benthic habitat map showing areas of the sea floor covered by coral reef, seagrass, hard bottom, and algae (NOAA et al. 2001). We isolated the coral reef polygons, created a new geodatabase feature class of those areas, and edited the attribute table to include categories for leeward or windward exposure (ESRI 2011).

Survey Methods

All sites were between 0.5 and 0.75 ha in area. We sampled each site with 3-8 haphazardly placed 30-m transects. We used SCUBA-based data collection methods adapted from those commonly used by the Atlantic and Gulf Rapid Reef Assessment (AGRRA) (Lang et al. 2010), Mesoamerican Barrier Reef Systems Project (MBRS) (Almada-Villela et al. 2003), and Reef Check (Hodgson et al. 2004). At each site, we used the point-intercept method to estimate the percent cover of major benthic taxa, including live hard coral; sea fans; branching soft corals; fleshy, filamentous, calcareous and crustose algae; erect and encrusting sponges; and substrates, such as sand and rubble (Almada-Villela et al. 2003). In addition, all scleractinian coral colonies intersected by the transect tape were identified to species, classified by morphology, and measured in length and maximum orthogonal width. We calculated coral colony density using the Strong Method, in which density (organisms/m^2)=Σ(1/M)(unit area/total transect length) where M is the maximum orthogonal width (Strong 1966, Bakus 2002). We also calculated the number of coral species recorded per transect, as a simple estimate of species richness that is adjusted for sampling effort. All individuals of the most common sea fan (*Gorgonia ventalina*) within a 1-m wide belt transect were measured for height and width. We calculated their density as the number of sea fans per m^2 using counts per transect.

To quantify the indirect effects of anchoring, we assessed reef complexity and fish population densities. The three-dimensional structural complexity (or rugosity) was estimated for each transect using the consecutive height difference method, for which the height of the tape off the bottom is measured every 50 cm and the variance in those heights used to describe vertical complexity (McCormick 1994). Reef-associated fish were counted using belt transects that were 45 m^2 in area (30 m x 1.5 m). We counted all small- to medium-sized diurnal fish species, excluding very small cryptic benthic species (e.g., some gobies and blennies) and very mobile mid-water species (e.g., jacks).

Calculations and Statistical Analyses

All statistical analyses were done using site means as replicates because chronic anchor damage is more appropriately assessed at a site level than at a transect level, and because sites are a meaningful unit for management.

We primarily used randomized block ANOVAs to assess the impact of anchoring. We tested effects of two categorical factors: anchoring activity, categorized as levels H-high, M-medium, and L-low, and group. Although sea fans were included in all surveys for benthic cover, specific measurements of sea fan density and size were made at fewer sites. Therefore, we classified medium sites as high for statistical analysis (n_L=7, n_H=8). Pairwise comparisons between anchoring activity levels were done using least squares means (LSM). When data were transformed to satisfy the ANOVA assumption of normality, we display anchoring level means and standard errors based on the untransformed data for ease of unit interpretation from the graphs. When the assumptions of Analysis of Variance (ANOVA) were not met, or that test was not appropriate, we used either nonparametric Kruskal-Wallis (K-W) tests with Nemenyi post-hoc tests or Maximum Likelihood Estimation (MLE) models using appropriate distributions to model the variance. MLE models were fitted with anchoring only, group only, and both anchoring and group as factors. Models were then compared using Akaike Information Criterion (AIC) and the parameters from the best fitting model were used to calculate means and standard errors for a more intuitive presentation of results (see Bolker 2008). When analyzing proportional data, we utilized a beta distribution with parameters ‘a’ and ‘b,’ from which you can calculate the mean $(a/(a+b))$ and the variance $(ab/((a+b)^2(a+b+1))$. For data that were positive and continuous, we utilized gamma and lognormal distributions. The gamma distribution resulted in ‘s’ (scale) and ‘a’ (shape) parameters, with which we calculated means (as) and variances (as^2). The lognormal distribution provided μ and σ parameters, with which we calculated means $(\exp(\mu+\sigma^2/2))$ and variances $(\exp(2\mu+\sigma^2)(\exp(\sigma^2)-1))$. Standard error was calculated as the square root of the variance. For ease of interpretation and comparison between anchoring intensities, we have reported parameter estimates, z-values, and p-values from models only comparing across anchoring levels. All analyses were conducted in R (v. 3.0.2, R Core Team 2013), using packages ‘bbmle’, ‘lsmeans’ and ‘PMCMR’.

Results

Sites differed in anchoring activity but not in other respects

From the marine habitat maps we examined, we estimated 24% of coral reef area in the British Virgin Islands is leeward in exposure, although this only a rough estimate of the fraction of reef that is safe to anchor near because exposure varies with the seasons and weather. For the 25 leeward reef sites we surveyed, we confirmed that they differed in levels of anchoring but found no differences in proximity to land-based stressors. Based on surveys of historical GoogleEarth satellite imagery, there have been more boats anchored at sites classified as high (0-11) anchoring than either medium (0-3) or low (0-5) (ANOVA F=12.8, $p<0.00001$) (Fig. 4). There were also more overturned corals (K-W $X^2=6.75$, p=0.034, Nemenyi $p_{H-L}=0.046$, $p_{H-M}=0.78$, and $p_{L-M}=0.625$), broken hard corals (K-W $X^2=8.67$, p=0.013, Nemenyi $p_{H-L}=0.048$, $p_{H-M}=0.72$, and $p_{L-M}=0.71$), and broken soft corals (square-root transformation, ANOVA F=10.18, p=0.002, LSM $t_{H-L}=4.40$, $p_{H-L}=0.002$, $t_{H-M}=1.83$, $p_{H-M}=0.20$, $t_{L-M}=-0.659$, $p_{L-M}=0.79$) at sites with greater anchoring activity. Sites classified as high, medium or low anchoring areas were all similar distances from both land (ANOVA F=0.5, p=0.60) and development (F=0.3, p=0.75) (Fig. 5).

Responses of benthic taxa to anchoring

Of the many benthic taxa accounted for in our sampling, only two showed a significant response to anchoring activity: hard coral cover and sea fan cover. Hard coral cover at highly anchored sites (10%) was only 58% of that at sites experiencing medium or little anchoring (17%) (MLE, beta distribution, a~Anchoring+Group, dAIC=0, weight=0.84; $a_H=9.48$, $z_H=2.76$, $p_H=0.006$; $a_{M-H}=8.13$, $z_{M-H}=1.98$, $p_{M-H}=0.047$; $a_{L-H}=8.56$, $z_{L-H}=2.3$, $p_{L-H}=0.02$; $a_{L-M}=0.44$, $z_{L-M}=0.14$, $p_{L-M}=0.89$; b=88.26, $z_b=2.82$, $p_b=0.0048$)(Fig. 6). Sea fan cover was best modeled with the ‘a’ parameter estimated solely by anchoring activity Sea fan cover at sites with high and medium levels of anchoring was only 39.1% of that at control sites (MLE, beta distribution, a~Anchoring, dAIC=0, weight=0.74; $a_H=1.42$, $z_H=2.56$, $p_H=0.01$; $a_{M-H}=-0.085$, $z_{M-H}=-0.12$, $p_{M-H}=0.9$; $a_{L-H}=2.54$, $z_{L-H}=2.02$, $p_{L-H}=0.044$; $a_{L-M}=2.62$, $z_{L-M}=1.97$, $p_{L-M}=0.049$; b=27.05, $z_b=2.70$, $p_b=0.0069$)(Fig. 6).

Responses of coral populations to anchoring

Coral colonies were 39% smaller (ANOVA F=7.16, p=0.007) at sites that experience high anchoring activity than at sites with medium or low levels (LSM H-L t ratio=-2.66, p=0.046; H-M t ratio=-1.59, p=0.28; L-M t ratio=-0.089, p=0.996) (Fig. 7). In addition, coral colony density was 57% lower at sites with high anchoring than at sites with little or no anchoring (MLE using lognormal distribution with μ~Anchoring; dAIC=0.0, df=4, weight=0.63; $\mu_{H}=2.06$, $z_{H}=12.1$, $p_{H}<0.00001$; $\mu_{M-H}=0.21$, $z_{M-H}=0.60$, $p_{M-H}=0.55$; $\mu_{L-H}=0.85$, $z_{L-H}=3.63$, $p_{L-H}=0.00028$; $\mu_{L-M}=0.64$, $z_{L-M}=1.82$, $p_{L-M}=0.068$; $\sigma=0.54$, $z_{\sigma}=6.93$, $p_{\sigma}<0.00001$) (Fig. 7). Species richness was also 42% lower at higher anchoring activity levels (either medium or high) than at low levels (ANOVA F=14.76, p=0.0004; LSM H-L t ratio=-5.4, p=0.0002; H-M t ratio=0.31, p=0.94; L-M t ratio=3.43, p=0.01) (Fig. 7).

Certain morphological types of corals were particularly affected by anchoring: branching (including *Acropora cervicornis, Madracis decactis, Porites divaricata, P. furcata,* and *P. porites*), mound (including *Dichocoenia stokesii, Favia fragum, Madracis pharensis, Orbicella annularis, O. cavernosa, O. faveolata,* and *O. franksii, P. astreoides, Siderastrea radians,* and *S. siderea*), and plate corals (*Agaricia agaricites, A. humilis,* and *A. lamarcki*). Mean branching coral colony size was 65% smaller where anchoring was greater (fifth root transformation, ANOVA, F=3.8047, p=0.05003; no significant LSM contrasts). Branching coral density was also 67% lower at high anchoring sites than at control sites (square root transformation, ANOVA F=3.9, p=0.047, LSM H-L t ratio=-2.75, p=0.041; H-M t ratio=-0.24, p=0.97; L-M t ratio=1.40, p=0.3673). Both the colony size of mound corals and their densities were 51% lower at sites with high anchoring than at control sites (size ANOVA F-26.83, p=0.00002, LSM H-L t ratio=-6.70, p<0.0001; H-M t ratio=-2.898, p=0.03; L-M t ratio=0.899, p=0.65; density MLE using lognormal distribution with μ~Anchoring, dAIC=0.0, df=4, weight=0.57; $\mu_{H}=1.66$, $z_{H}=9.90$, $p_{H}<0.00001$; $\mu_{M\text{-}H}=0.14$, $z_{M\text{-}H}=0.40$, $p_{M\text{-}H}=0.69$; $\mu_{L\text{-}H}=0.72$, $z_{L\text{-}H}=3.09$, $p_{L\text{-}H}=0.002$; $\mu_{M\text{-}L}=-0.58$, $z_{M\text{-}L}=-1.67$, $p_{M\text{-}L}=0.10$; $\sigma=0.53$, $z_{\sigma}=6.93$, $p_{\sigma}<0.00001$). Plate coral size did not differ between anchoring intensities, but colony density was 55% lower at high anchoring sites (MLE using gamma distribution with s~Anchoring and a~Group, dAIC=0, df=11, weight=0.93; $s_{H}=1.50$, $z_{H}=3.23$, $p_{H}=0.0012$; $s_{M\text{-}H}=-0.33$, $z_{M\text{-}H}=-0.51$, $p_{M\text{-}H}=0.61$; $s_{L\text{-}H}=1.82$, $z_{L\text{-}H}=2.23$, $p_{L\text{-}H}=0.026$; $s_{M\text{-}L}=-2.14$, $z_{M\text{-}L}=-2.16$, $p_{M\text{-}L}=0.03$; $a_{Average}=1.69$). Brain corals, cup-like corals, and encrusting coral sizes and densities did not differ across anchoring intensity regimes.

The lower colony sizes and densities at higher anchoring levels were attributed to four of the most commonly encountered genera, *Agaricia* spp. (which accounts for all plate corals), *Orbicella* spp., *Porites* spp., and *Siderastrea* spp., plus the rare genera (any besides those listed or *Solenastrea* sp.). The mean colony size and density of members of the genus *Orbicella* were 48% and 70% lower at highly anchored sites, respectively (size: ANOVA, F=13.61, p=0.0005, LSM H-L t ratio=04.63, p=0.001; H-M t ratio=-2.44, p=0.07; L-M t ratio=0.18, p=0.98; density: square root transformation, ANOVA, F=4.54, p=0.03, LSM H-L t ratio=-3.11, p=0.02; H-M t ratio=-0.51, p=0.87; L-M t ratio=1.27, p=0.44). The colony size and density of *Porites* spp. were both lower at highly anchored sites, by 40% and 45%, respectively (size: MLE using a lognormal distribution with μ~Anchoring+Group, dAIC=0.0, df=11, weight=0.67; $\mu_{H}=3.98$, $z_{H}=25.09$, $p_{H}<0.00001$; $\mu_{M-H}=-0.33$, $z_{M-H}=-0.99$, $p_{M-H}=0.32$; $\mu_{L-H}=0.50$, $z_{L-H}=2.28$, $p_{L-H}=0.023$ $\mu_{M-L}=-0.83$, $z_{M-L}=-2.53$, $p_{M-L}=0.01$; $\sigma=0.50$, $z_{\sigma}=6.93$, $p_{\sigma}<0.00001$; density: MLE with gamma distribution and s~Anchoring, dAIC=0, df=4, weight=0.90; $s_{H}=2.85$, $z_{H}=3.32$, $p_{H}=0.0009$; $s_{M-H}=-0.20$, $z_{M-H}=-0.20$, $p_{M-H}=0.84$; $s_{L-H}=2.35$ $z_{L-H}=2.19$, $p_{L-H}=0.028$; $s_{M-L}=-2.54$, $z_{M-L}=-1.94$, $p_{M-L}=0.052$; a=0.69, $z_{a}=3.37$ $p_{a}=0.0008$). *Siderastrea* spp. coral colony size was 78% lower but density does not differ between anchoring levels (size: MLE using a lognormal distribution with μ~Anchoring, dAIC=0.0, df=4, weight=0.89; $\mu_{H}=4.28$, $z_{H}=14.90$, $p_{H}<0.00001$; $\mu_{M-H}=1.17$, $z_{M-H}=1.96$, $p_{M-H}=0.050$; $\mu_{L-H}=1.52$, $z_{L-H}=3.83$, $p_{L-H}=0.00013$; $\mu_{M-L}=-0.34$, $z_{M-L}=-0.58$, $p_{M-L}=0.56$; $\sigma=0.91$, $z_{\sigma}=6.93$, $p_{\sigma}<0.00001$). The colony size and density of rare genera were 58% and 75% lower at highly anchored sites compared to little anchored ones (size: cube root transformation, ANOVA, F=3.84, p=0.047, none of the LSM contrasts were significant; density: cube root transformation, ANOVA, F=4.02, p=0.042, LSM H-L t ratio=-2.893, p=0.03, H-M t ratio=-1.48, p=0.33, L-M t ratio=0.16, p=0.99).

Responses of sea fan populations to anchoring

Gorgonia ventalina density was 42% lower at highly anchored sites than at control sites (ANOVA, F=8.91, p=0.017). Mean height and width were 28% and 25% lower at high anchoring sites, respectively (height ANOVA F=16.93, p=0.0044; width ANOVA F=5.83, p=0.046).

Changes in reef structure due to anchoring

Rugosity at sites with high anchoring activity was 40% lower than that at sites with little or no anchoring (MLE using lognormal distribution with μ~Anchoring+Group; dAIC=0.0, df=11, weight=1; $\mu_H=4.66$, $z_H=55.36$, $p_H<0.00001$; $\mu_{M-H}=0.41$, $z_{M-H}=2.61$, $p_{M-H}=0.009$; $\mu_{L-H}=0.49$, $z_{L-H}=4.18$, $p_{L-H}=0.00003$; $\mu_{M-L}=-0.075$, $z_{M-L}=-0.49$, $p_{M-L}=0.63$; $\sigma=0.27$, $z_\sigma=7.07$, $p_\sigma<0.00001$) (Fig. 8).

Fish Populations

Mean total fish density was 55% lower at sites with high anchoring than at sites with little or no anchoring, changing from 110 to 49 fish/45m^2 (ANOVA F=6.26, p=0.01); sites with medium anchoring activity had intermediate densities (LSM H-L t ratio=-3.8, p=0.005, H-M t ratio=-1.3, p=0.4, L-M t ratio=1.2, p=0.48) (Fig. 9). The density of adult fish was 66% lower: 82 fish/45m^2 at sites with little anchoring but only 29 at highly anchored sites (ANOVA F=8.45, p=0.004), similarly with intermediate densities at intermediate levels of anchoring (LSM H-L t ratio=-4.4, p=0.002, H-M t ratio=-1.9, p=0.2, L-M t ratio=1.0, p=0.58). However, juvenile fish density did not differ by anchoring level. Fish species richness was 35% lower at highly anchored sites than at sites with little or no anchoring, declining from an average of 23 species/45m^2 to 15 (ANOVA F=10.7, p=0.002), with an intermediate richness index at site with medium anchoring levels (LSM H-L t ratio=-5.1, p=0.0004, H-M t ratio=-0.9, p=0.6, L-M t ratio=2.5, p=0.06) (Fig. 9).

These reductions in fish density were spread across several specific functional groups. The density of adult herbivores (parrotfish, surgeonfish, and damselfish) was 68% lower at sites with high anchoring than at sites with little or none (ANOVA F=9.4, p=0.003). The density at medium sites is intermediate between those at either highly or little anchored sites (LSM H-L t ratio=-4.4, p=0.002, H-M t ratio=-2.1, p=0.14, L-M t ratio=0.82, p=0.7) (Fig. 10). There were 61% fewer piscivores (groupers, lizardfish and lionfish) (MLE using lognormal distribution with μ~Anchoring+Group; dAIC=0.0, df=11, weight=0.63; μ_{H}=-0.011, z_{H}=-0.06, p_{H}=0.96; μ_{M-H}=0.94, z_{M-H}=2.5, p_{M-H}=0.012; μ_{L-H}=0.81, z_{L-H}=2.85, p_{L-H}=0.004; μ_{M-L}=0.13, z_{M-L}=-0.34, p_{M-L}=0.73; σ=0.64, z_{σ}=6.93, p_{σ}<0.00001) (Fig. 10). There were also 73% fewer adult scrapers (stoplight, queen, and blue parrotfish), at highly anchored sites with intermediate densities of scrapers at medium sites (ANOVA F=5.03, p=0.02; LSM H-L t ratio=-3.8, p=0.006, H-M t ratio=-1.4, p=0.4, L-M t ratio=1.1, p=0.5) (Fig. 10). Spongivore (angelfish, filefish, spadefish, and boxfish) densities were 95% lower at highly anchored sites than at low anchoring sites (K-W X^2=12.6, p=0.002; Nemenyi $_{pH-L}$=0.003, p_{H-M}=0.4, p_{M-L}=0.4). Finally, highly anchored sites had 36% fewer benthic carnivores (wrasse, butterflyfish, hamlets, groupers, bass, pufferfish, grunts, goatfish, drum, snappers, trunkfish, triggerfish, mojarra, porgy, and porcupine fish) per unit area, with densities similar at sites with medium and low levels of anchoring (MLE using lognormal distribution with μ~Anchoring; dAIC=0.0, df=4, weight=0.62; μ_{H}=2.01, z_{H}=13.9, p_{H}<0.00001; μ_{M-H}=0.57, z_{M-H}=2.1, p_{M-H}=0.03; μ_{L-H}=0.44, z_{L-H}=2.2, p_{L-H}=0.03; μ_{M-L}=0.13, z_{M-L}=-0.48, p_{M-L}=0.63; σ=0.46, z_{σ}=6.93, p_{σ}<0.00001) (Fig.10).

Discussion

Clearly, anchor damage contributed to reef decline in the BVI. We have documented that chronic anchoring reduced coral cover; coral and sea fan colony size and density; coral species richness; reef structural complexity; and fish density and richness. Coral cover of 17% at our sites with little or no anchoring corresponded to the current Caribbean-wide average of 16.8% (Jackson et al. 2014). The 10% cover at highly anchored sites falls well below that, as cover at these anchored sites was only about 60% of what it is at sites without anchoring. For context, it has been estimated that a single hurricane can reduce absolute coral cover by 17% the year after it occurs in the Caribbean (Gardner et al. 2005), as well as reduce cover proportionally by 31.5% following storms, 42.2% following crown-of-thorns starfish outbreaks, 12.2% due to disease, and 13.9% due to bleaching in the Great Barrier Reef (Osborne et al. 2011). However, all of those values represent the effects of an acute event, so care must be taken in comparing them to the 7% absolute and 40% proportional reduction of coral cover we attribute to chronic anchoring activities. The magnitude of the differences between sites with chronic anchoring and those without was substantial, and larger than we had expected given the BVI's established network of mooring buoys dating to the 1970s (personal communication, Lianna Jarecki, Guana Science, BVI). Currently, there are 66 sites with 200 moorings managed by the National Parks Trust in the BVI (personal communication, Nancy Pascoe, National Parks Trust of the Virgin Islands), plus a number of "unofficial" moorings not overseen by the National Parks Trust.

The magnitude of decline in coral cover and species diversity could greatly affect the future outlook for reefs. Connell (1997) showed that corals recover less frequently from chronic, long-term disturbances than from acute ones. Reefs exposed to chronic local anthropogenic stressors exhibit diminished growth rates—and thereby fitness—and resilience to acute events, such as bleaching episodes (Carilli et al. 2009).

The loss of biodiversity that we documented may alter ecosystem performance, particularly once major changes in functional groups occur (Naeem et al. 1994).

The loss of coral that we documented is substantial enough to represent a change of habitat that may impact fish and other mobile organisms. Reefs with higher cover of live coral typically support greater reef fish abundance and species richness (Garpe and Öhman 2003); and this pattern is evident in our data. For some species the specific mechanisms for this dependence on live coral have been uncovered. Juveniles of one species of damselfish on dead coral engage in riskier behaviors and do not respond to predator cues from injured conspecifics, resulting in a large reduction in survival (Lönnestedt *et al.* 2014). We saw that juvenile fish occurred in similar densities across anchoring activity levels but that adult densities were lower where anchoring was higher. This may be due to increased juvenile mortality or, alternatively, emigration of adults. Competitive interactions may also be altered with habitat decline by increasing agonistic interactions, changing the density-dependence of mortality, and modifying competitive dominance hierarchies (Boström-Einarsson et al. 2014). In addition, physically disturbed reefs often have lower three-dimensional complexity (Fava et al. 2009), and the structural complexity of the reef is also highly correlated with fish abundance and diversity (McCormick 1994). Reef fish abundance and species richness decline where reefs have reduced structural complexity, usually because many fish use structure as shelter and for nesting sites (Gratwicke and Speight 2005a; Gratwicke and Speight 2005b, Friedlander and Parrish 1998). Through reductions in the size and density of branching and plate-like morphologies, the types and varieties of refuge spaces available for fish and mobile invertebrates is also reduced. Our results show several indirect effects of anchoring on various fish functional groups. Of particular interest are the declines in herbivores and scrapers. Loss of herbivory is ecologically significant because it has been linked to higher cover of algae and further reduction in coral cover (Mumby 2006, Burkepile and Hay 2008). Contrary to predictions, however, we did not find any differences in algal cover across the gradient of anchoring activity. Mumby (2006) estimated that only 10-30% of reef can be kept in a grazed state by parrotfish. A reduction of parrotfish should reduce that area grazed and allow algal overgrowth. However, it may be that anchoring's direct disturbance of the substrate reduces algal growth and this, coupled with the remaining herbivore activity, maintains algal levels similar to those maintained by herbivory alone on undisturbed reef. All told, the indirect effects of anchoring on fish populations are substantial and could contribute to a loss of overall ecosystem function and services.

There are some limitations to our study and its interpretability. While 4 sites were designated as medium in their level of anchoring activity based on expert opinion, we have made our comparisons between high and low levels because the medium level had a smaller sample size, higher variance, and represented a less well-resolved category. The responses at these sites are consistent with the expectation that they would fall within the bounds of low and high. We do report values for medium on graphs as their inclusion suggests trends, such as cases in which responses appear to be linear along a gradient of anchoring (when medium is intermediate), highly vulnerable to anchoring (when medium clusters with high) or more robust to anchoring (when medium clusters with low). While we do believe our study is replicable, for comparison across studies, more refined enumeration of boat anchoring at sites may be required. Finally, our study represents a single snapshot in time of the influence of anchoring on coral habitat. It is likely that anchoring has already interacted with other stressors at the site and may have diminished anchored reefs' recovery from bleaching events (Carilli et al. 2009). Long-term monitoring studies that assess damage from various sources would provide further information on the relative contribution of anchoring to coral decline compared to other stressors, such as hurricanes or bleaching events. Such monitoring studies may also be able to assess whether chronic anchoring does indeed diminish reef resilience (Carilli et al. 2009).

Where anchoring is affecting reefs, increasing efforts to reduce its impact may be a worthwhile investment of time and money because changing anchoring behavior represents a more tractable management problem than some global stressors of coral reefs, such as climate change. To prevent possible damage caused by anchors and their chains, many governments have established networks of moorings buoys (Project AWARE and PADI International, Inc. 1996). However, it has also been suggested that mooring buoys may attract more visitors to reefs; therefore, it is necessary to ensure that the moorings are not attracting more damage than they alleviate (Hocevar 1993). One case study in Florida reported a lower percentage of injured corals in buoyed sites than nearby areas, even though buoyed sites were visited more frequently (Hocevar 1993). In our study, most highly anchored sites also had moorings but were still degraded compared to sites with little anchoring, most of which had no moorings.

An alternative to use of moorings is to designate no-anchoring zones and utilize marker buoys to show which areas are designated as such. That approach has been effective in reducing incidence of anchoring damage on the Great Barrier Reef (Beeden et al. 2014). In the BVI, reefs on the leeward sides of islands are most vulnerable to anchor damage. Because only one quarter of reefs in the BVI are leeward in exposure, management plans should prioritize those reefs for additional moorings or zoning.

Educational programs raising awareness of anchor damage may reduce its impact, because education has been used successfully to ameliorate other harmful side-effects of tourist behavior. For example, a study of diver damage to reefs found that informational dive briefings about conservation lowered diver incursions with the reefs (Camp and Fraser 2012). It may be that educating boat users about the impact anchors can have on coral reefs may encourage them to change behaviors and thereby reduce impacts (Poonian 2008). Incorporating education with mooring and monitoring programs that rate charters on their compliance with best practices may also be effective, as seen in the Green Fins program in South East Asia (Hunt et al. 2013). In addition, sharing information that demonstrates the dramatic effect of anchoring on reefs, such as the results of this study, with tourists and local stakeholders alike may galvanize local conservation efforts. Regardless of which management strategy is chosen, it is important to document the effectiveness as a tool to minimizing reef damage. It would be informative to understand under what circumstances various tactics work and why they do not in others.

Since anchor damage appears to be a substantive contributor to coral reef decline in the BVI, but its effects elsewhere are poorly documented, we argue that it is worthwhile to assess anchoring impacts in other areas with significant boating activity.

Using the negative impact of anchoring to coral reefs as an example, we can comment on the importance of identifying and assessing local sources of habitat decline. They may contribute more to habitat decline than expected. While global drivers of habitat decline are important, local stressors are often easier to manage and focusing on them may help ignite local interest and involvement in conservation efforts. Managing locally may increase local habitat resilience and preserve valuable ecosystem functions and services.

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Figure Legends

Figure 1. Locations of reefs surveyed around the British Virgin Islands. The shade of the point indicates whether it was categorized as a site with high, medium, or low anchoring frequency.

Figure 2. An example of historical imagery from GoogleEarth to show how we counted anchored boats. The pin represents a mooring buoy, so this image has 1 moored vessel and 1 anchored one.

Figure 3. An example of using GoogleEarth to measure distance to shore. The site is indicated by the pin (White Bay Mega-Peter)—a highly anchored site in White Bay of Peter Island. The line is the shortest distance to shore (0.51 km). Similar measurements were made to nearest shore and nearest development for all sites.

Figure 4. There have been more boats anchored at sites classified as high than at low based on GoogleEarth historical imagery. Our classification based on expert opinion is on the x-axis and the number of boats per image is on the y. Error bars represent standard error. Significant differences are indicated with letters.

Figure 5. There are no significant differences between anchoring levels in sites' proximity to shore (left) or development (right). Error bars represent standard error.

Figure 6. Hard coral and sea fan cover differ across anchoring levels. Cover is shown as a proportion of the bottom habitat. Darker bars indicate hard coral cover while lighter ones refer to sea fan cover. The error bars represent the standard errors of the means calculated from the parameters from the MLE analysis. Letters indicate statistically significant differences within each type of cover: 'a' and 'b' for hard coral and 'c' and 'd' for sea fans.

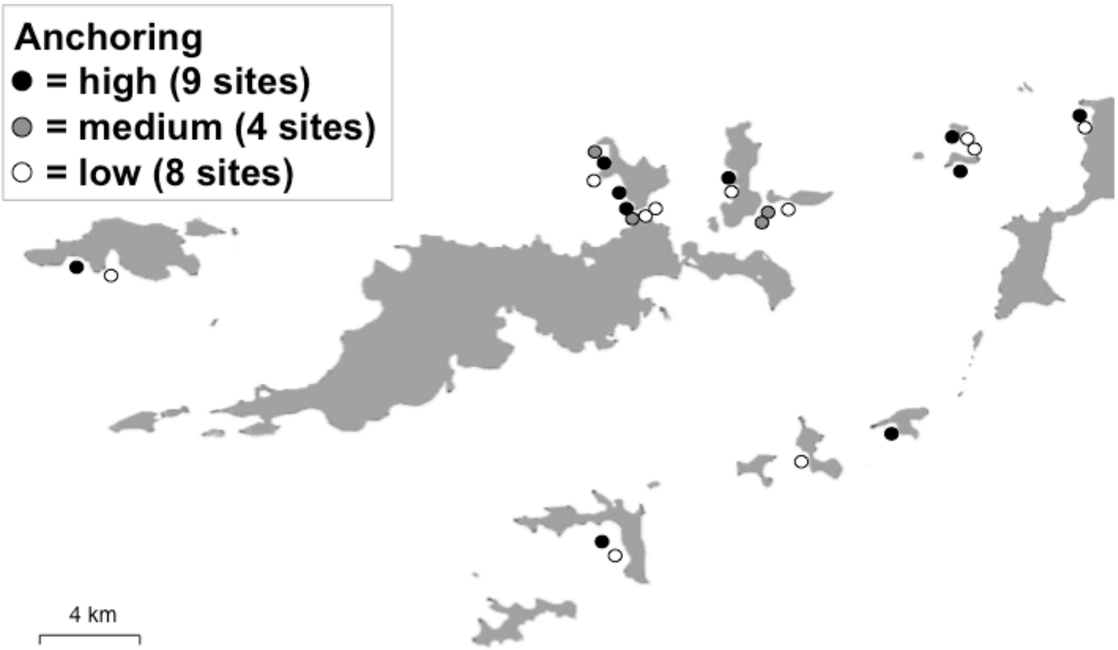
Figure 7. (A) Coral colony size, (B) density, (C) coral species richness and (D) coral abundance differ across anchoring levels. All error bars represent standard error. Significant differences are indicated with letters on each graph.

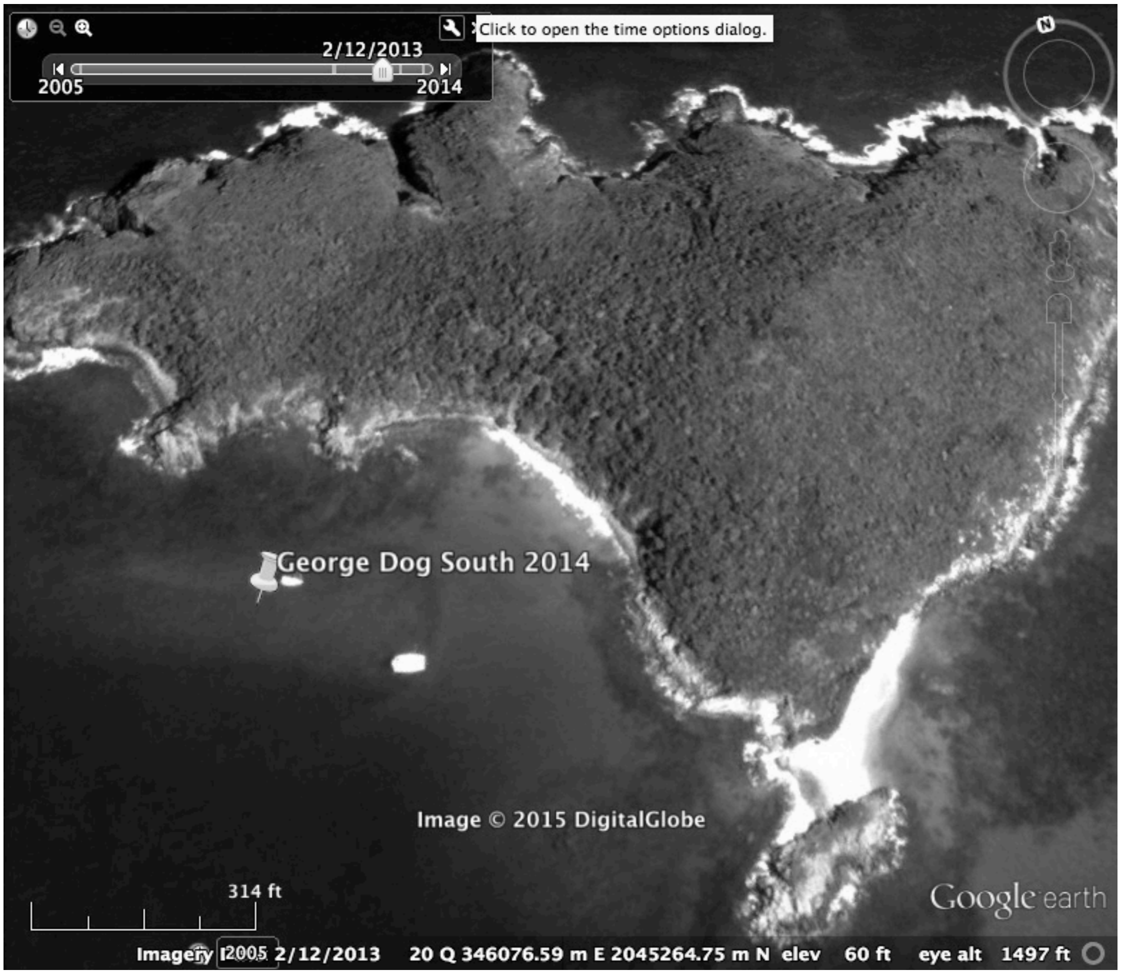
Figure 8. Rugosity declines as anchoring increases. Standard error is indicated with capped bars. The letters indicate statistically significant differences.

Figure 9. Fish density (left) and richness (right) diminish with increased anchoring activity. Standard error is indicated with capped bars. The letters indicate statistically significant differences.

Figure 10. Different functional groups are affected differently by anchoring. (A) Adult herbivores, (B) adult scrapers, (C) piscivores, and (D) benthic carnivores all experience a decline with increased anchoring but the magnitude varies. Standard error is indicated with capped bars. The letters indicate statistically significant differences.

Figures

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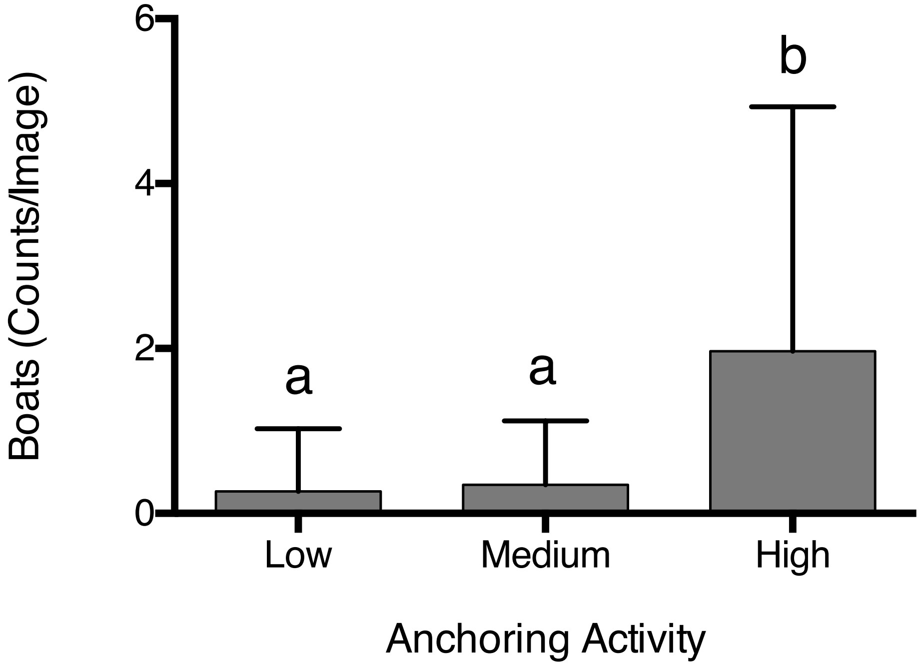

Boats (Counts/Image)
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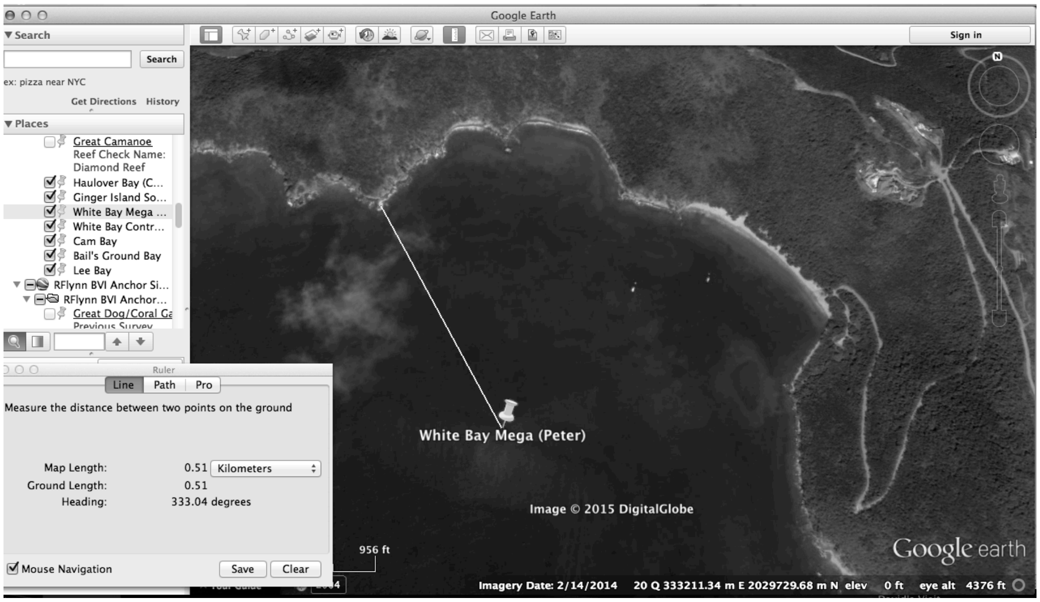

Measure the distance between two points on the ground

Map Length: 0.51 Kilometers

Ground Length: 0.51

Heading: 333.04 degrees

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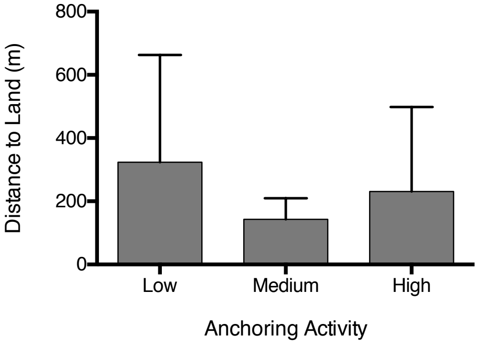
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Low
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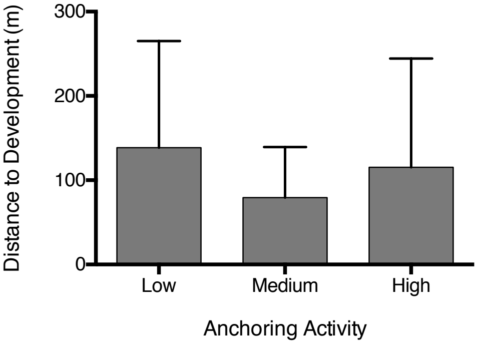
Anchoring Activity


Distance to Development (m)
300
200
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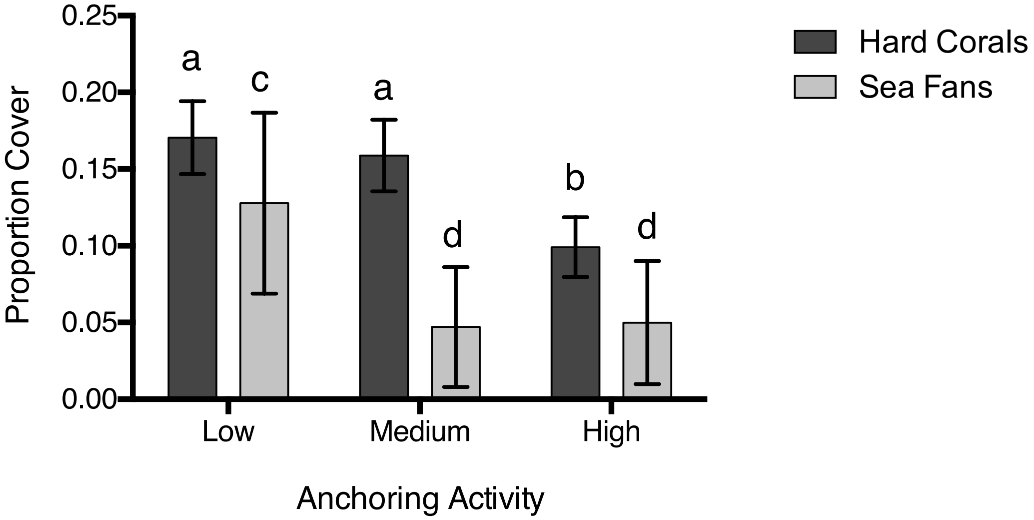
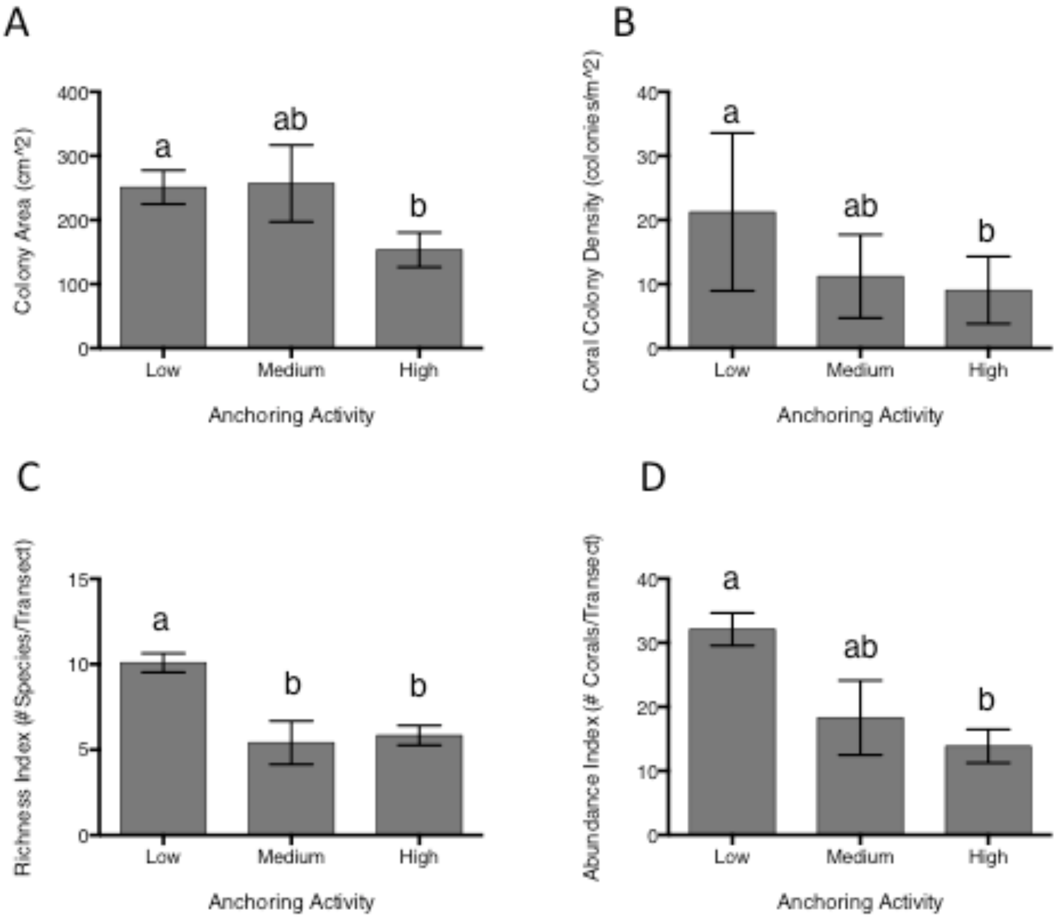
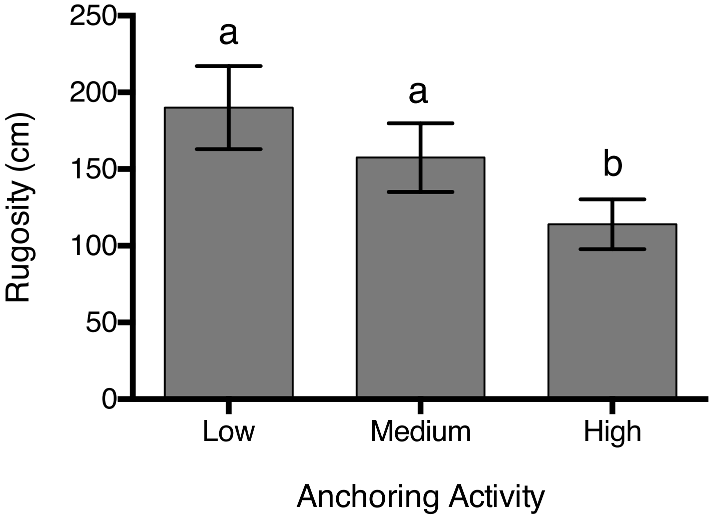
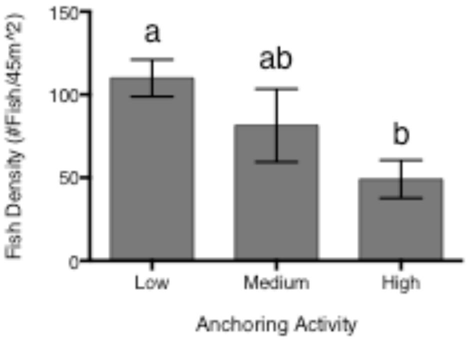
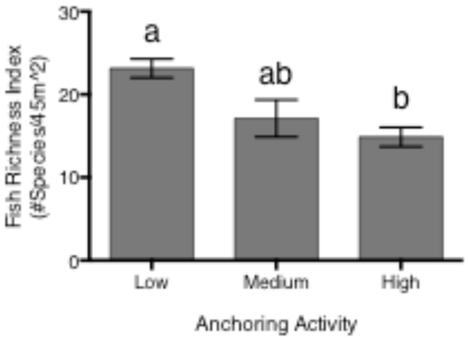
High
Anchoring Activity

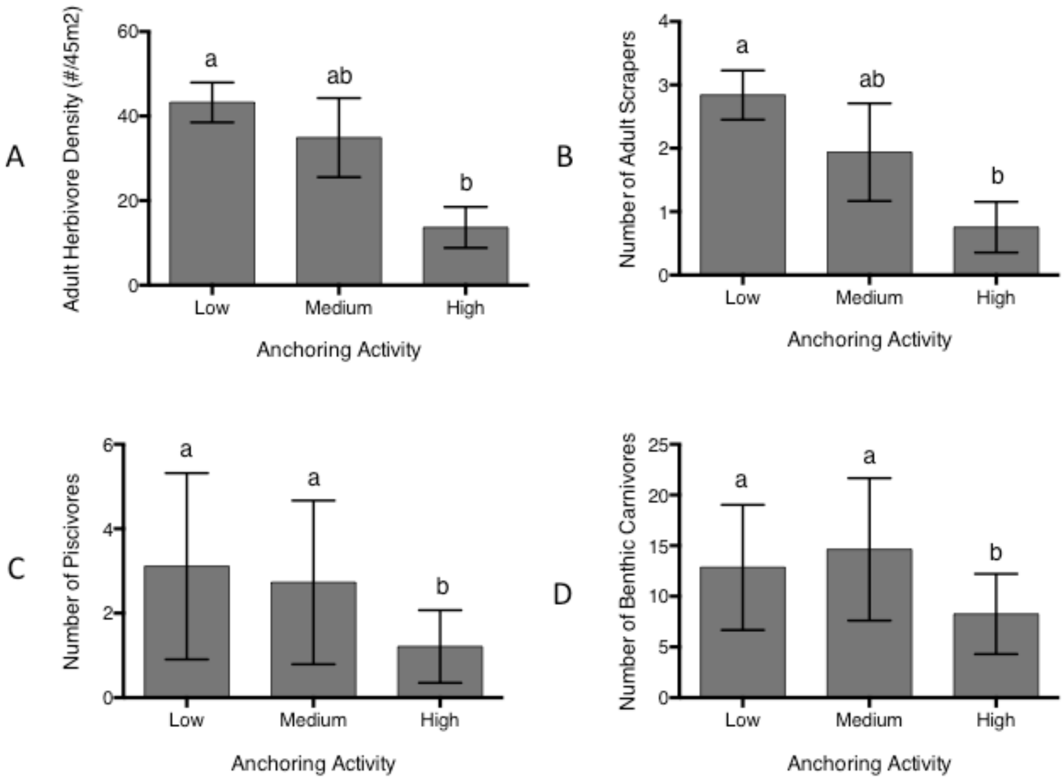

0.25
0.20
0.15
0.10
0.05
0.00
Proportion Cover
a
c
a
d
b
d
Low
Medium
High
Anchoring Activity
Hard Corals
Sea Fans


A
Colony Area (cm^2)
0
100
200
300
400
a
ab
b
Low
Medium
High
Anchoring Activity
B
Coral Colony Density (colonies/m^2)
0
10
20
30
40
a
ab
b
Low
Medium
High
Anchoring Activity
C
Richness Index (# Species/Transect)
0
5
10
15
a
b
b
Low
Medium
High
Anchoring Activity
D
Abundance Index (# Corals/Transect)
0
10
20
30
40
a
ab
b
Low
Medium
High
Anchoring Activity


250
200
150
100
50
0
Rugosity (cm)
a
a
b
Low
Medium
High
Anchoring Activity


Fish Density (#Fish/45m^2)
150
100
50
0
a
ab
b
Low
Medium
High
Anchoring Activity


Fish Richness Index (#Species/45m^2)
30
20
10
0
a
ab
b
Low
Medium
High
Anchoring Activity


A
Adult Herbivore Density (#/45m2)
60
40
20
0
a
ab
b
Low
Medium
High
Anchoring Activity
B
Number of Adult Scrapers
4
3
2
1
0
a
ab
b
Low
Medium
High
Anchoring Activity
C
Number of Piscivores
6
4
2
0
a
a
b
Low
Medium
High
Anchoring Activity
D
Number of Benthic Carnivores
25
20
15
10
5
0
a
a
b
Low
Medium
High
Anchoring Activity