The Impact of Anchor Damage Relative to Other Causes of Habitat Change on Coral Reefs

El Impacto de los Daños de Anclaje con Respecto a Otras Causas de Cambio de Hábitat en Los Arrecifes de Coral

L'Impact des Dommages de Cheville par Rapport aux Autres Causes de Changement de l'Habitat sur les Récifs Coralliens

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ABSTRACT

Reef degradation is caused by the integrative effects of natural disturbances (e.g. hurricanes) and anthropogenic stressors, including climate-change, fishing, pollution, and recreation. As water-based recreation increases so does the risk of anchor damage to coastal habitats, yet reef decline due to anchor damage is little understood and poorly documented. We used two approaches to assess the impact of anchor damage relative to other drivers of change on coral reefs in the British Virgin Islands. First, at one site that was monitored for 22 years, a one-time destructive anchoring event by a large vessel caused coral loss of a similar magnitude to chronic declines from other causes. Second, a synoptic survey of 25 sites that varied in how frequently boats anchored near reef revealed that anchoring explains a substantial fraction of the spatial variation in benthic community composition. In combination, these results indicate that anchor damage can have a substantial impact on coral reefs and habitat for fishes. In areas with frequent boat traffic, increased effort to mitigate this damage may thus be a worthwhile investment.

KEY WORDS: Anchoring, habitat, coral decline

INTRODUCTION

Coral reefs habitats have high biodiversity, 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, such as supporting 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 (Graham et al. 2009, Lewis 1998).

Reef degradation is caused by the integrative effects of natural disturbances (e.g. hurricanes) and anthropogenic stressors (Wilkinson and Buddemeier 1994, Wilkinson 2008). Key anthropogenic stressors include global climate change (ocean warming and acidification), invasive species, and local effects from fishing, pollution, and recreation (Wilkinson 2004, 2008). As one consequence of a rise in tourism, boat traffic is increasing rapidly in many areas (Burgin and Hardiman 2011, Davenport and Davenport 2006). For example, in the British Virgin Islands (BVI), there are now 1,100 - 1,500 charter yachts operating in 60 square miles of water (Janet Oliver, BVI Charter Yacht Society, personal communication). Because the species richness of reef-building scleractinian corals is determined by both local and regional processes, anchoring may potentially impact coral assemblages (Cornell and Karlson 1996). In addition, many global stressors, such as global climate change, are difficult to combat, at least in the short-term. In principle, reducing the effects of physical anchor damage should represent a much more tractable management problem.

Boat anchoring has long been acknowledged as a source of damage to coral reefs (Goenaga 1991), but, compared to other human impacts, has been the subject of virtually no formal study (Johnstone et al. 1998). A search of Web of Science for *coral reef and anchor* returns only 68 papers. For comparison, a search for *coral reef and climate* returns 2,335 and one for *coral reef and fishing* returns 6,234. Several of those 68 papers do little more than mention anchoring, noting that a dragging anchor likely fragmented and overturned colonies (Glynn 1994) or that their study site was damaged by boat anchoring (Öhman et al. 1993). The mechanisms by which anchors cause damage have been detailed, such as dislodging after the anchor catches hold (McManus et al. 1997), overturning coral heads (Dinsdale and Harriott 2004, Glynn 1994), and crushing corals (Fava et al. 2009). Researchers have considered possible metrics for anchor damage (Dinsdale and Harriott 2004), but the few estimates of loss of coral cover due to anchoring are highly variable (between 0.3%/year and 7%/year (McManus et al. 1997, Saphier and Hoffmann 2005)) and may be based on unrealistic assumptions. A more accurate, but unreplicated, estimate revealed that coral species richness on an anchor-damaged Indonesian was reduced by 10% at 10 m depth and 50% at 3 m depth relative to control reefs (Edinger et al. 1998). Anchoring may impact organisms other than corals since the crushing of corals can contribute to reef flattening and loss of refuges (Fava et al. 2009). For instance, Lewis (1998) damaged corals experimentally as part of a controlled experiment, and found that localized damage lead to the extirpation of some reef fish that live only in live coral.

In addition, anchor damage is implicated in shifting community assemblages. Anthropogenically disturbed reefs have diminished resilience, and often shift to communities dominated by non-coral taxa, such as macroalgae (Dudgeon et al. 2010). Modeling shows the potential for fishermen who anchor by dropping rocks to lower coral cover and trigger a shift in the community from a coral-dominated to macroalgae-dominated state (Maynard et al. 2010). The results of field observations and experiments support that outcome. For example, Rogers and Garrison (2001) found that macroalgae accounted for the highest percent cover of organisms colonizing a cruise-ship anchor scar, even ten years after the event. Even though coral recruitment was high in the scar, coral survival and growth were poor, likely due to changing flow patterns that created continually shifting sediments within the scar (Rogers and Garrison 2001). It is also possible that the algae outcompeted the juvenile corals colonizing the scar. In experimental reef plots, all benthos was cleared to simulate anchor damage (Schlöder et al. 2013). Coral recovery in experimental plots was slow and rare, and most plots shifted to macroalgal domination (Schlöder et al. 2013).

Although informative, these few 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 importance of rigorous comparisons between anchor-damaged coral reefs and undamaged sites. Our objective, therefore, was to determine the impact of anchor damage on coral reefs relative to other factors. We used two approaches to assess the effect of anchoring. First, we analyzed long-term coral cover data from a site damaged by a large (50 m) vessel in a single anchoring event. Second, we conducted a spatial survey of 25 leeward reefs that varied in the amount of regular anchoring activity by smaller vessels.

METHODS

Study Area

We studied the impact of anchoring in the British Virgin Islands (BVI) because communication with industry professionals suggested it has one of the highest densities of charter yachts (12 - 16 m length) in the world. This fleet is growing rapidly, as is visitation by larger "mega-yachts," that exceed 45 m in length. The large number and size of boats contribute to a high risk of anchor damage to coral reefs.

Site-specific Effects of a Single Anchoring Event by a 50 m Vessel

This analysis isolates the impact of a single severe anchoring event at one site (Crab Cove, near Guana Island, BVI) that has been monitored annually from 1992 to the present (Figure 1). The monitoring site is roughly 0.6 ha and is surveyed every year by divers. Fish are counted using 30 x 1.5 m belt transects, and benthic species using 30 m point intercept transects. Each year, 3 - 6 transects are placed at haphazard locations within the site. On 7 July 2004, a 50 m vessel called the Holo-Kai anchored overnight near the site. On 08 July, the reef was assessed and mapped by divers, showing that heavy chain from the three anchors deployed caused damage to roughly 1.5 ha of reef, including roughly 50% of the monitoring site. Documentation of the damage revealed several symptoms of anchor damage: overturned, broken, and scarred coral colonies as well as bent and broken soft corals. Using the map of the damaged area, and records of the placement of each transect each year, all transects from 1992 - 2013 were categorized as either inside or outside of the anchor-damaged area. Although unintentional, the anchoring event created a design similar to that often used to assess unreplicated environmental impacts (i.e. Before-After-Control-Impact designs). To isolate the effect of the anchoring event, we used a linear mixed model with two repeated factors. The first repeated factor was year of sampling and the second was before vs. after the anchoring event (i.e. years were classified into two groups - those before and those after the anchor damage). The model also included a categorical anchor damage factor: whether transects were inside or outside the anchor-damaged part of the site. We also included an additional factor *zone*, in which transects were assigned to one of two sub-areas within the monitoring site according to distance from the shore. The zone factor was included simply to account for a spatial gradient of increasing coral cover with increasing distance from shore (Friedlander and Parrish 1998). Our main interest was, however to test for an interaction between the *inside versus outside* and *before versus after* effects, which, if significant, would indicate an impact of the 2004 anchoring event.

BVI-wide Effects of Chronic Anchoring

In summer 2014, we conducted a spatial survey of 25 reefs in the BVI to assess the effect of chronic anchoring. Sites were chosen to represent a gradient of anchoring activity, and were classified as experiencing either little or no anchoring (n = 11), medium (n = 4) or high (n = 10) anchoring (Figure 1). Classification was based on plausibility of use as an anchorage, expert opinion, and presence of symptoms of anchor damage. Plausible anchoring sites are leeward reefs, 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, and sites selected for study were those about which there was consensus of opinion about the extent of anchoring. Once in water, divers surveyed for the symptoms of anchor damage to corroborate the experts' assessments. Control (little or no anchoring) sites were situated geographically close to

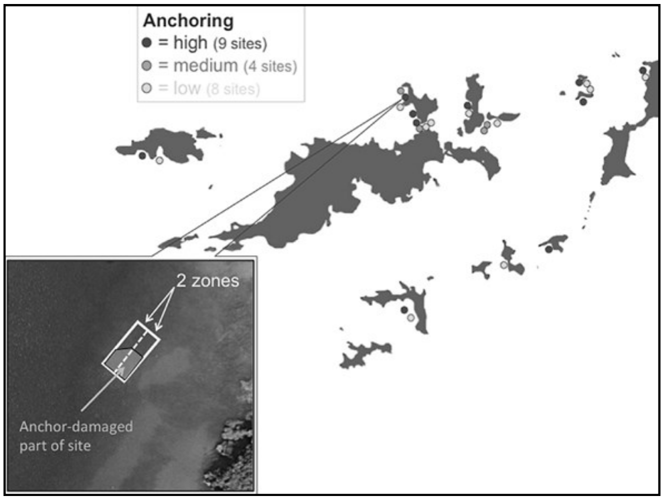

Figure 1. Map of our Study Area, including a pop out of Crab Cove. The map of the British Virgin Islands has circles indicating our survey sites from 2014. The dark dots show high intensity anchoring sites, gray dots show medium intensity anchoring sites, and light dots indicate low anchoring intensity sites. The picture shows the two Crab Cove zones and the portion of the long-term monitoring site damaged in 2004.

anchor damaged sites but were rarely anchored based on expert assessment and lack of damage symptoms. Typically, these sites were not used as anchorages because they were too close to a shallow reef, a rock wall, or some other hazard for safe anchoring. To account for other sources of variation, sites were assigned to groups that were in close proximity geographically, and were similar in characteristics such as depth, wave exposure, and reef slope.

All sites were between 0.5 and 0.75 ha in area, and each was sampled using 3 - 8 haphazardly placed 30 m transects. We used SCUBA-based data collection methods adapted from those commonly used by AGRRA (Lang et al. 2010), MBRS (Almada-Villela et al. 2003), and Reef Check (Hodgson et al. 2004). At each site, percent cover of major benthic taxa was assessed using point-intercept counts along the transects. Reef three-dimensional structural complexity (or rugosity), was estimated for each transect using the consecutive height difference method (McCormick (1994). To estimate coral colony density, we measured the maximum orthogonal width of each colony intercepted by the tape, and used these measurements to calculate density using the Strong Method (Strong 1966, Bakus 2002). Each intercepted colony was identified to species, and we used the number of species recorded per transect as an index estimate of species richness that was corrected for sampling effort.

We used randomized block ANOVAs to test the effect of anchoring. The two factors were anchoring activity (low, medium, and high), and group (used as a blocking factor). Site averages of each dependent variable were used as replicates because, for management purposes, damage at the site-scale is more relevant than damage at the level of individual transects. The dependent variables examined were percent live coral cover, rugosity, coral colony density, and coral species richness. Rugosity and coral colony density were square root transformed prior to analysis to satisfy the normality assumption of ANOVA.

RESULTS

Site-specific Effect of a Single Anchoring Event by a 50 m Vessel

The key result from the mixed linear model was a significant interaction between the *inside versus outside* and *before versus after* effects (df = 1,64, F = 63.4, p = 0.012). Inspection of Figure 2 illustrates the cause of the interaction. Outside of the area affected by the Holo-Kai anchoring event, percent coral cover showed a progressive decline over time from 1992 - 2013. This gradual decline also occurred within the area damaged by the Holo-Kai, but here there is also an abrupt loss of coral that occurred right after the anchoring event. Within the damaged area, comparing the marginal means for percent coral cover before the damage (24%) to that after (12%) provides a crude but simple estimate of the magnitude of the anchoring impact — a reduction in coral cover of 12%. Between 1992 and 2013, there was an overall coral cover decline from 33% to 8% inside the anchor-damaged area — a reduction in coral cover of 25%. Therefore, almost half of the overall decline was attributable to the one-time anchoring event in 2004.

BVI-wide Effects of Chronic Anchoring

When we compared 25 sites around the BVI, all measures of reef composition were significantly reduced as the level of anchoring increased. Percent live coral cover was highest at low anchoring sites, lower where anchoring occurred at intermediate levels, and lowest at high anchoring sites (Figure 3; ANOVA df = 2, F = 9.67, p = 0.007). Likewise, reef structural complexity was highest at sites with low levels of anchoring, intermediate at medium levels, and lowest at high levels (Figure 4; ANOVA df = 2, F = 18.39, $p < 0.0001$). Coral colony density was higher at low levels of anchoring intensity than at medium or high levels, which had similar densities (Figure 5; ANOVA df = 2, F = 6.56, $p < 0.009$). Like colony density, coral species richness was also higher at sites with low anchoring and similarly low at sites with medium and high anchoring levels (Figure 6; df = 2, F = 16.91, p = 0.00018).

DISCUSSION

Although we are not able to precisely estimate the impacts of boat anchoring relative to other causes of coral decline, it is clear that anchor damage is a substantial contributor to the loss of coral over the past 22 years in the BVI. The Holo-Kai event showed that the amount of coral mortality inflicted in one night by a large vessel can almost equal the cumulative loss over 22 years caused by all other factors combined. Given that background decline at Crab Cove is likely in part due to chronic anchoring by small yachts, our estimate of anchoring's impact at this site is conservative. The loss of coral cover attributed to the Holo-Kai in one night (12%) is also substantial relative to the total change in coral cover over 22 years at seven other BVI sites. At these seven other BVI sites, the mean percent cover declined from 30% in 1992 to 18% in 2013 — a change of 12%. Moreover, the Holo-Kai impact is also

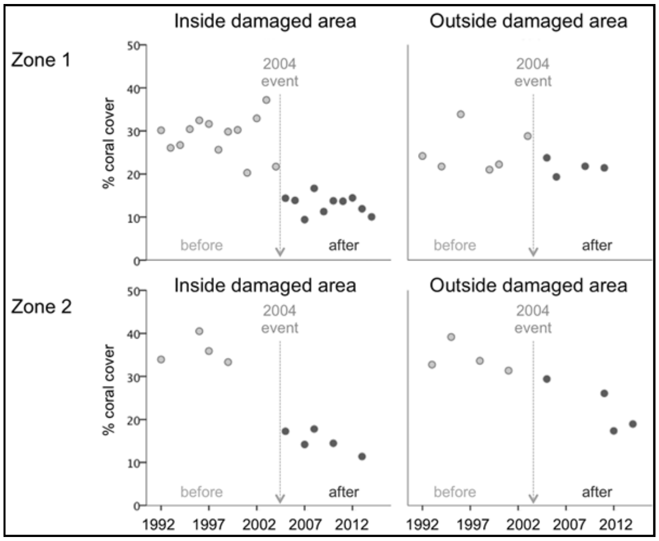

Figure 2. Change in coral cover at Crab Cove over time. The vertical line indicates the 2004 anchoring event. Zones 1 and 2 area sub-sections of the site that are closer and further from the shore respectively (see Figure 1).

substantial relative to recent Caribbean-wide estimates of long-term coral decline. Averaged across 88 locations region-wide, percent coral cover was recently estimated to have declined from 35% in 1970 to 16% in 2011 — a loss of 19% in 40 years (Jackson et al. 2014).

The BVI-wide survey also points to a substantial impact of anchoring. In this case, based on our casual observations and the comments from local experts, we suspect most of the impact is attributable to the cumulative effect of recurrent anchoring by smaller charter yachts (12-16 m length). The mean coral cover at sites with little or no anchoring was 18%, whereas at sites classified as *high* anchoring areas it was 8%—a difference in coral cover of roughly 10%. Again, quantifying the relative effect of anchor damage and other drivers of change is difficult, but as context we note that mean coral cover at the low anchoring sites (18%) is close to the current regional average of 16% (Jackson et al. 2014). A cumulative anchoring effect that has reduced coral cover by 10% at the high anchoring sites is thus a substantial impact.

In order to best isolate the effect of anchor damage, all 25 sites we surveyed were as similar as possible in all respects except for the level of anchoring. All of the *control* sites were, therefore, leeward reefs with similar physical structure to those used as anchorages. In order to better assess the overall impact of anchoring, it would be informative to also sample windward reefs that, because they are exposed to prevailing winds, are rarely used as anchorages. Including windward reefs would then allow estimation of the overall fraction of reef area that is anchor damaged.

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

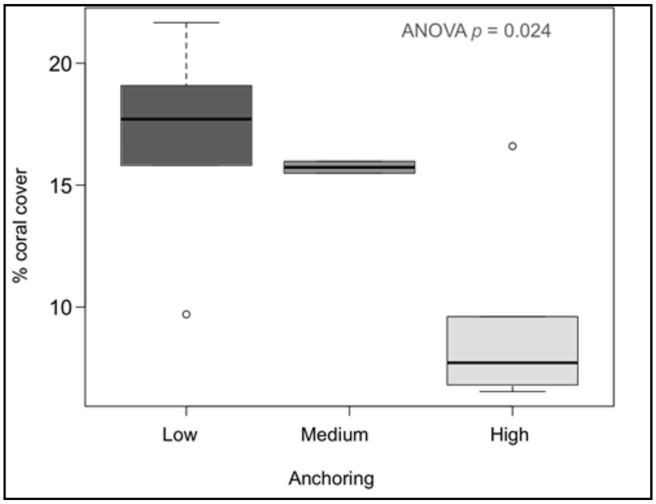

Figure 3. Box and whisker plot showing how % coral cover varies by anchoring intensity. Plots show median, interquartile range, range and extreme values.

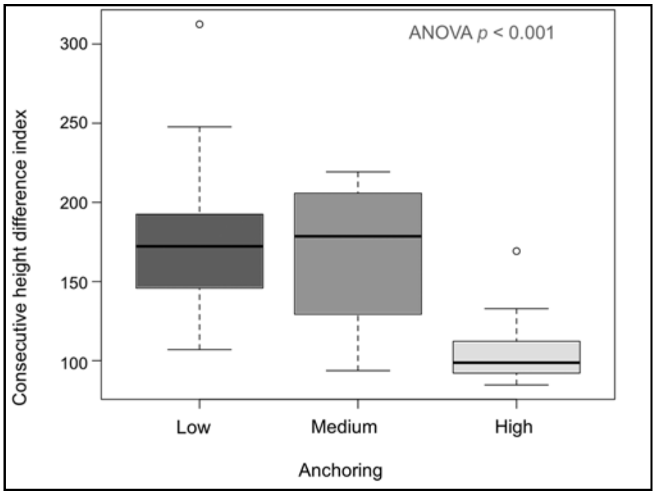

Figure 4. Box and whisker plot showing how rugosity varies by anchoring intensity. Plots show median, interquartile range, range and extreme values.

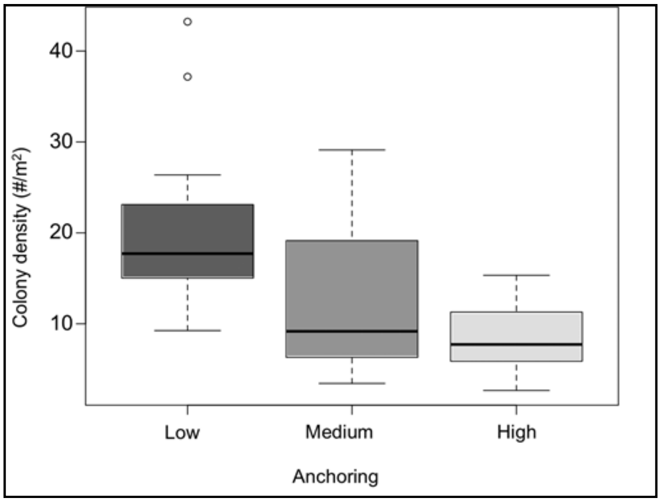

Figure 5. Box and whisker plot showing how coral colony density varies by anchoring intensity. Plots show median, interquartile range, range and extreme values.

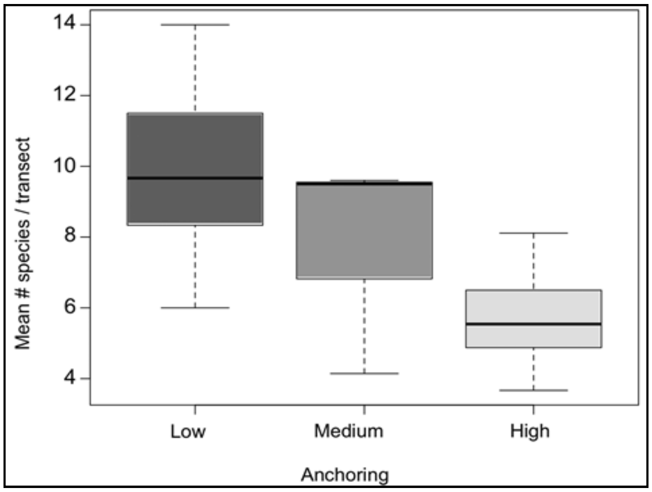

Figure 6. Box and whisker plot showing how coral species richness varies by anchoring intensity. Plots show median, interquartile range, range and extreme values.

of live coral typically support greater reef fish abundance and species richness (Garpe and Öhman 2003). For some species the specific mechanisms for this dependence on live coral have been uncovered. Some damselfish on dead coral, for example, do not respond to predator cues from injured conspecifics and place themselves at risk of predation by increasing their distance from shelter and spending longer outside of shelter than conspecifics on live coral (Lönnestedt et al. 2014). These changes translated to a reduction in survival, since fish on dead coral habitats experienced 75% lower survival than those on live coral (Lönnestedt et al. 2014). 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 declines 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).

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. 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. 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 (Poonian 2008). 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 and charter companies about the impact anchors can have on coral reefs may encourage them to change behaviors and thereby reduce impacts. To prevent possible damage caused by anchors and their chains, many governments have established networks of mooring buoys (Project AWARE and PADI International, Inc. 1996). Moorings can be used to help implement zoning plans for management, limit numbers of visitors, and may be removed or relocated to allow specific reefs to recover (Project AWARE and PADI International, Inc. 1996). 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). However, it has also been suggested that because mooring buoys may attract more visitors to reefs, it is necessary to ensure that the moorings are not attracting more damage than they alleviate (Hocevar 1993). Anecdotal reports suggest that in the BVI, some yachts will anchor near mooring fields if all buoys are in use, whereas others still choose to anchor even when moorings are available. Moorings are thus a potentially effective way to ameliorate damage from yacht anchoring, but should be coupled with educational and monitoring programs to encourage their proper use.

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LITERATURE CITED

Almada-Villela, P.C., P.F. Sale, G. Gold-Bouchot, and B. Kjerfve. 2003. *Manual of Methods for the MBRS Synoptic Monitoring Program: Selected Methods for Monitoring Physical and Biological Parameters for Use in the Mesoamerican Region*. Mesoamerican Barrier Reef Systems Project (MBRS). Belize City, Belize. 155 pp.

Alvarez-Filip, L., N.K. Dulvy, J.A. Gill, I.M. Côté, and A.R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society Biological Sciences Series B* **276**:3019-3025.

Bakus, G.R. 2002. *Quantitative Analysis of Marine Biological Communities: Field Biology and Environment*. Wiley Interscience, Hoboken, New Jersey USA. 35 pp.

Burgin, S. and N. Hardiman. 2011. The direct physical, chemical and biotic impacts on Australian coastal waters due to recreational boating. *Biodiversity Conservation* **20**:683-701.

Burke, L., K. Reytar, M. Spalding, and A. Perry. 2011. *Reefs at Risk Revisited*. World Resources Institute, Washington, DC. USA. 115 pages.

Camp, E. and D. Fraser. 2012. Influence of conservation education dive briefings as a management tool on the timing and nature of recreational SCUBA diving impacts on coral reefs. *Ocean & Coastal Management* **61**:30-37.

Cornell, H.V. and R.H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* **65**(2):233-241.

Davenport, J. and J.L. Davenport. 2006. The impact of tourism and personal leisure transport on coastal environments: a review. *Estuarine, Coastal and Shelf Science* **67**:280-292.

Dinsdale, E.A. and V.J. Harriott. 2004. Assessing anchor damage on coral reefs: a case study in selection of environmental indicators. *Environmental Management* **33**(1):126-139.

Dudgeon, S.R., R.B. Aronson, J.F. Bruno, and W.F. Precht. 2010. Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series* **413**:201-216.

Edinger, E.N., J. Jompa, G.V. Limmon, W. Widjatmoko, and M.J. Risk. 1998. Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. *Marine Pollution Bulletin* **35**(8):617-630.

Fava, F., M. Ponti, A. Scinto, B. Calcinai, and C. Cerrano. 2009. Possible effects of human impacts on epibenthic communities and coral rubble features in the marine Park of Bunaken (Indonesia). *Estuarine, Coastal and Shelf Science* **85**:151-156.

Friedlander, A.M. and J.D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* **224**:1-30.

Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant, and A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**:958-960.

Garpe, K.C. and M.C. Öhman. 2003. Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish-habitat interactions. *Hydrobiologia* **498**:191-211.

Glynn, P.W. 1994. State of coral reefs in the Galápagos Islands: natural vs anthropogenic impacts. *Marine Pollution Bulletin* **29**(1-3):131-140.

Goenaga, C. 1991. The state of coral reefs in the wider Caribbean. *Interciencia* **16**(1):12-20.

Graham, N.A.J., S.K. Wilson, M.S. Pratchett, N.V.C. Polunin, and M.D. Spalding. 2009. Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodiversity Conservation* **18**: 3325-3336.

Gratwicke, B. and M.R. Speight. 2005a. The relationship between fish species richness, abundance, and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* **66**:650-667.

Gratwicke, B. and M.R. Speight. 2005b. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* **292**:301-310.

Hocevar, J.D. 1993. A Survey of the Stony Coral Community Composition of Pompano Ledge, Broward County, Florida, with a Preliminary Evaluation of the Effectiveness of Mooring Buoys in Reducing Coral Damage. M.S. Thesis. Nova Southeastern University, Fort Lauderdale, Florida USA. 121 pp.

Hodgson, G., W. Kiene, J. Mihaly, J. Liebeler, C. Shuman, and L. Maun. 2004. Reef Check Instruction Manual: *A Guide to Reef Check Coral Reef Monitoring*. Reef Check, Institute of the Environment, University of California at Los Angeles, Los Angeles, California USA. 92 pp.

Jackson, J.B.C., M.K. Donovan, K.L. Cramer, and V.V. Lam (eds.). 2014. *Status and Trends of Caribbean Coral Reefs: 1970-2012*. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland. 306 pp.

Johnstone, R.W., C.A. Muhando, and J. Francis. 1998. The status of the coral reefs of Zanzibar: one example of a regional predicament. *Ambio* **27**(8):700-707.

Lang, J.C., K.W. Marks, P.A. Kramer, P.R. Kramer, and R.N. Ginsburg. 2010. AGRRA Protocols Version 5.4. Atlantic and Gulf Rapid Reef Assessment. University of Miami, Miami, FL USA. 31 pp.

Lewis, A.R. 1998. Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs. *Journal of Experimental Marine Biology and Ecology* **130**:91-110.

Lönnestedt, O.M., M.I. McCormick, D.P. Chivers, and M.C.O. Ferrari. 2014. Habitat degradation is threatening reef replenishment by making fish fearless. *Journal of Animal Ecology* **83**:1178-1185.

Maynard, J.A., K.R.N. Anthony, S. Afatta, N. Dahl-Tacconi, and O. Hoegh-Guldberg. 2010. Making a model meaningful to coral reef managers in a developing nation: a case study of overfishing and rock anchoring in Indonesia. *Conservation Biology* **24**(5):1316-1326.

McCormick, M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* **112**:87-96.

McManus, J.W., R.B. Reyes, Jr., and C.L. Nañola, Jr. 1997. Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environmental Management* **21**(1):69-78.

Öhman, M.C., A. Rajasuriya, and O. Lindén. 1993. Human disturbances on coral reefs in Sri Lanka: a case study. *Ambio* **22**(7):474-480.

Poonian, C.N.S. 2008. The influence of protected area management on the status of coral reefs at Misali Island, Tanzania following the 1998 bleaching event in the western Indian Ocean. *African Journal of Ecology* **46**:471-478.

Project AWARE and PADI International, Inc. 1996. *Mooring Buoy Planning Guide*. International PADI, Inc. Rancho Santa Margarita, CA. 92 pp..

Rogers, C.S. and V.H. Garrison. 2001. Ten years after the crime: lasting effects of damage from a cruise ship anchor on a coral reef in St. John, U.S. Virgin Islands. *Bulletin of Marine Science* **69**(2):793-803.

Saphier, A.D. and T.C. Hoffmann. 2005. Forecasting models to quantify three anthropogenic stresses on coral reefs from marine recreation: anchor damage, diver contact, and copper emission from antifouling paint. *Marine Pollution Bulletin* **51**:590-598.

Schlöder, C., A. O'Dea, and H.M. Guzman. 2013. Benthic community recovery from small-scale damage on marginal Caribbean reefs: an example from Panama. *Bulletin of Marine Science* **89**(4):1003-1013.

Schutte, V.G.W., E.R. Selig, and J.F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* **402**:115-122.

Strong, C.W. 1966. An improved method of obtaining density from line-transect data. *Ecology* **47**(2):311-313.

Wilkinson, C. (ed.). 2004. *Status of Coral Reefs of the World: 2004. Volume 1*. Australian Institute of Marine Science, Townsville, Australia. 316 pp.

Wilkinson, C. (ed.). 2008. *Status of Coral Reefs of the World: 2008*. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia. 298 pp.

Wilkinson, C.R. and R.W. Buddemeier. 1994. *Global Climate Change and Coral Reefs: Implications for People and Reefs.* Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on the Implications of Climate Change on Coral Reefs. IUCN, Gland, Switzerland. 134 pp.