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Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot



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ARTICLE INFO

Article history:
Received 28 August 2014
Received in revised form
8 November 2014
Accepted 13 November 2014
Available online 15 November 2014

Keywords:
Coral reefs
Diseases
Koh Tao
Ecosystem management
Marine parks
Scuba diving
Snorkelling
Sediments
Tourism

ABSTRACT

While coral reefs are increasingly threatened worldwide, they are also increasingly used for recreational activities. Given the environmental and socio-economic significance of coral reefs, understanding the links between human activities and coral health and evaluating the efficacy of marine protected areas (MPAs) as a management regime to prevent further deterioration are critically important. The aim of this study was to quantify indicators of coral health at sites inside and outside a newly rezoned MPA framework in the dive tourism hotspot of Koh Tao, Thailand. We found that patterns in the health and diversity of coral communities one year on did not reflect the protected status conferred by newly zoned MPAs, but instead reflected past history of recreational use around the island. Sites characterised as past high-use sites had lower mean percent cover of hard corals overall and of corals in the typically diseaseand disturbance-susceptible family Acroporidae, but higher mean cover of species in the more weedy family Agariciidae. Past high use sites also had higher mean prevalence of infectious diseases and other indicators of compromised health. Sites within the newly established MPAs are currently subjected to higher levels of environmental and anthropogenic pressures, with sedimentation, algal overgrowth, feeding scars from Drupella snails, and breakage particularly prevalent compared to sites in non-MPA areas. Given the greater prevalence of these factors within protected sites, the capacity of the MPA framework to effectively prevent further deterioration of Koh Tao's reefs is unclear. Nevertheless, our study constitutes a strong baseline for future long-term evaluations of the potential of MPAs to maintain coral health and diversity on highly threatened reefs.

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1. Introduction

The accelerating pace of coral loss worldwide (Selig and Bruno, 2010; De'ath et al., 2012) and the need to understand the underlying causes of the declines are now widely recognised. There is no single cause but rather multiple factors acting alone or in synergy, such as rising sea surface temperatures (SSTs), ocean acidification, and nutrient run-off (Jackson et al., 2001; Harvell et al., 2007; Hoegh-Guldberg et al., 2008; Burke et al., 2012). All of these factors are likely to increase the impact of coral diseases on reef community structure and associated ecosystem services, highlighting disease as another issue of growing concern. First

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described in the Caribbean in the 1970's (reviewed in Sutherland and Ritchie, 2004), coral diseases have now been shown to affect reefs worldwide and are increasingly threatening Indo-Pacific coral reefs (Harvell et al., 2007; Willis et al., 2004; Myers and Raymundo, 2009; Weil et al., 2012), even at remote uninhabited reefs (Vargas-Angel, 2009; Williams et al., 2011a,b). However, research on coral disease is still in its infancy and there have been consistent calls for further studies on causes of the increasing frequency of disease outbreaks worldwide and on measures for their mitigation, including the potential of marine protected areas (MPAs) to ameliorate coral health (Richardson, 1998; Harvell et al., 1999, 2007; Raymundo et al., 2009; Roder et al., 2013).

Links between a range of environmental factors and increasing disease prevalence suggest a role for changing climate in the rise of coral diseases. In particular, recent studies suggest a link with global warming and rising SSTs (Harvell et al., 2002; Bruno et al.,

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2007; Sato et al., 2009; Heron et al., 2010; Maynard et al., 2011; Ruiz-Moreno et al., 2012). Evidence of rising disease prevalence following bleaching events (Bruno et al., 2007; Maynard et al., 2011) and seasonal patterns of disease outbreaks (Sato et al., 2009; Haapkyla et al., 2011) also indicate that disease levels can be high in the absence of local human pressures. Climate warming could have the dual effect of increasing pathogen virulence while decreasing coral host resilience (Harvell et al., 2002, 2007; Bruno et al., 2007; Heron et al., 2010; Ruiz-Moreno et al., 2012). Other abiotic factors associated with climate change, such as ocean acidification (Williams et al., 2014), and anthropogenic stressors, such as escalating human population sizes and decreased water quality (Pollock et al., 2014), can act synergistically with sea temperature warming to further impede corals' resistance to infectious diseases (Harvell, 2007; Hoegh-Guldberg et al., 2008; Danovaro et al., 2008; Van der Meij et al., 2010).

The role of human-related activities in coral disease dynamics is poorly understood but likely to be highly complex (Harvell, 2007, 2009). Loss of ecosystem complexity through overfishing, increased nutrient-run off associated with coastal development, and activities like dredging that increase sedimentation, have all been proposed as potential causes of disease outbreaks (Kaczmarsky, 2006; De'ath and Fabricius, 2010; van der Mey et al., 2010; Aeby et al., 2011; Haapkyla et al., 2011; Lamb and Willis, 2011; Ruiz-Moreno et al., 2012; Pollock et al., 2014). Recently, links between coral disease and human activities in areas of high tourist visitation (Danovaro et al., 2008; Lamb and Willis, 2011; Onton et al., 2011: Lamb et al., 2014) highlight reef-based activities as an additional cause for concern. Snorkelling and diving activities may cause breakage of coral colonies, reducing corals' resistance to infections (Page et al., 2009; Guzner et al., 2010; Lamb and Willis, 2011; Onton et al., 2011 Lamb et al., 2014). Recreational activities on coral reefs may also introduce new pathogens or further increase pollution and nitrification (e.g. fish feeding, sunscreen) (Danovaro et al., 2008; Lamb and Willis, 2011). There is thus a crucial need to understand the links between human activities and coral health to better manage coral reefs worldwide (Lamb and Willis, 2011; Onton et al., 2011; Lamb et al., 2014).

In Thailand, 70% of annual tourism income is related to coastal marine activities (Sethapun, 2000). The island of Koh Tao alone receives more than 300,000 visitors a year, of which at least 60% participate in scuba diving or snorkelling activities (Nichols, 2013). Over the last decade, the island has become the centre of scuba diver training in southeast Asia, and hosts the second largest dive industry in the world, with over 50 dive schools responsible for fully one-third of all PADI certifications issued globally in 2009 (Wongthong and Harvey, 2014). Therefore, diving pressure far exceeds the recommended carrying capacity of a coral reef for scuba diving (5000-6000 divers/year; Hawkins and Roberts, 1997; Zakai and Chadwick-Furman, 2002). Moreover, supporting such a flourishing scuba diving industry has required rapid coastal development at the expense of the preservation of the Island's natural resources. Related human impacts caused by deforestation of coastal areas for tourist accommodation, overexploitation of fishing resources and poor sewage treatment are now putting further pressure on the Island's coral reefs (Wilkinson and Brodie, 2011; Weterings, 2011; Scott, 2012). Reefs surrounding Koh Tao were also severely affected by 2 mass bleaching events in 1998 and 2010 (Yeemin et al., 2006; Chavanich et al., 2012). A study investigating the impacts of marine-based recreational activities on coral health around the Island shortly after the 2010 bleaching event found a 3fold increase in disease prevalence at high use sites (Lamb et al., 2014), underscoring the need for strategies to manage recreational impacts on coral health and the potential of management

interventions to increase reef resilience following bleaching disturbances.

To address threats related to tourism expansion on Koh Tao, a group called "Save Koh Tao" (SKT) in conjunction with the Prince of Songkla University and the Thai Department of Marine and Coastal Resources (DMCR) designed and implemented a coastal zoning, regulatory and management plan for the Island in July of 2012 (Platong et al., 2012). Included in this plan was the establishment of an MPA covering the northwest quadrant of the Island and a new designation for a 300 m radius around Shark Island (see Fig. 1). The areas designated as MPAs around Koh Tao had previously been zoned as 'Protection' or 'Conservation' areas as early as 1988, but locals were largely unaware of the designation and there was little to no enforcement (Szuster and Dietrich, 2014). The new MPAs are designated as strict No-Take areas, primarily to address high fishing pressure at these sites, but with hoped-for, flow-on effects for coral health as a consequence of reduced fishing-related injuries.

The effectiveness of MPAs, in general, is a much-debated topic (Jameson et al., 2002; Halpern, 2003; Degnbol et al., 2006; Graham et al., 2011), and their capacity to mitigate coral disease is even more questionable (Coelho and Manfrino, 2007), although in some cases, lack of compliance confounds the interpretation of their role in ameliorating coral health (Page et al., 2009). Apart from Raymundo et al. (2009), who found decreased coral disease inside reserves, most studies indicate a general failure of MPAs to address the rising incidence of coral disease (Coelho and Manfrino, 2007; McClanahan et al., 2008; Page et al., 2009). They argue that coral diseases are associated with threats, like rising ocean temperatures, which are beyond the scope of protection provided by Marine

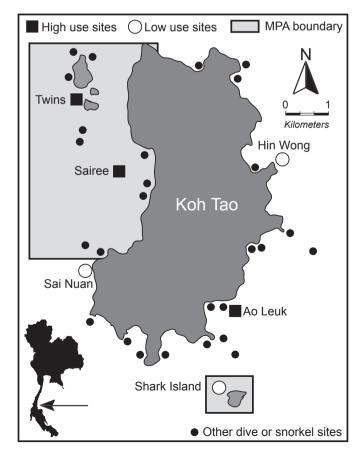


Fig. 1. Map showing locations of the six study sites around the Island of Koh Tao, Thailand. Grey squares delimit the MPA framework. Black squares represent past highuse sites; White circles represent past low-use sites.

Protected Areas. Moreover, MPAs could actually promote the spread of coral diseases if they successfully increase coral host density without controlling the spread of pathogens that are promoted through pollution, terrestrial run-off and increased tourist visitation in a warming ocean (Bruno et al., 2007; Page et al., 2009; Lamb and Willis, 2011). Nevertheless, although MPAs alone may not be able to mitigate disease outbreaks and coral loss worldwide related to warming and acidifying oceans, well-managed no-take zones have the potential to improve coral health by reducing fishing-related damage to corals. Improving our understanding of how MPAs affect the complex array of biotic and abiotic factors influencing disease prevalence in coral populations, particularly the timescale for production of potential beneficial results, is needed to provide local governing bodies with the information necessary to optimise the management of coral reefs.

In this study, we quantified indicators of coral health at sites inside and outside Marine Protected Areas surrounding the Island of Koh Tao, Thailand. More specifically, we compared coral cover and coral disease prevalence at MPA and non-MPA sites one year after the protected framework had been established to evaluate if the coral community was responding to the new protection status or if patterns in coral health reflected past high versus low use history. Comparing patterns in hard coral cover, taxonomic diversity, and disease prevalence among protected and unprotected sites enables us to provide a strong baseline of the health status of coral communities under the current management scheme and to identify links with specific local threats.

2. Methods

2.1. Study sites and field surveys

Coral health surveys were conducted on the reefs of Koh Tao during early August to late September 2013. A total of 6 sites were surveyed around the island. Three sites were located within the new MPA framework: Shark Island, Sairee, and Twins; and three sites were located outside the MPA framework: Ao Leuk, Hin Wong, and Sai Nuan (Fig. 1). Sites were also graded and categorised as past "high-use" or "low-use" sites, using records of site-specific disturbances in the six-year period between 2006 and 2012 (Fig. 1). Grades were determined by the New Heaven Reef Conservation Program Director (C. Scott), who has been qualitatively surveying these reefs since 2006, and were based on low to high levels of sedimentation, diving pressure, snorkelling pressure, waste-water run-off, and boat traffic. The potential impact of each of these five factors was scored as either low (1), medium (2) or high (3), giving a total score ranging between 5 and 15. Sites with a total score greater or equal to 10 were classified as past "high-use" sites, while sites with a total score less than 10 were classified as past "low-use" sites. Within the MPAs surveyed, 2 out of 3 sites (Sairee and Twins) are past high-use sites, while 2 out of 3 sites outside the MPA framework (Hin Wong and Sai Nuan) are past low-use sites (Fig. 1).

Each of the six sites was surveyed on SCUBA along three replicate 15 m \times 2 m belt transects. Transects were placed haphazardly at depths from 2.5 to 6 m, where coral communities are most abundant, and laid parallel to depth contours, with a minimum distance of 5 m between them. All corals within each of the 30 m² belt transects were recorded to the genus level and assigned to one of the following categories (as per Beeden et al., 2008): 1) diseased (black band disease, white syndromes, brown band disease, skeletal eroding band, growth anomalies, or unusual (non-focal) bleaching patterns), 2) showing other signs of compromised health (overgrown by algae and/or sponges; predation scars from fish, *Drupella* snails and/or crown-of-thorns starfish; or broken (tips or

whole fragments)), or 3) healthy (no visible signs of disease or other indicators of compromised health). Coral cover was estimated using the line-intercept method by recording every coral under each transect line to the genus level and measuring the distance it covered along the line to the nearest centimetre.

Sediment accumulation was measured by placing three sediment traps at each study site at a depth of 4–6 m. Sediment traps were 10 cm long and 3 cm wide PVC tubes, which were positioned approximately 5 cm above the substrata and left on site for 2–6 weeks. The traps had a height to width ratio of 3.3, which is close to the 3.6 ratio recommended to maximise sediment retention within the trap (Gardner, 1980). Once traps were recovered, sediments were filtered using Whatman glass microfiber filters (GF/C grade, 25 mm, 1.2 μ m) (Whatman, GE Healthcare, Little Chalfont, England) and dried. The contents of traps were then transported to Mahidol University in Bangkok, where they were dried and weighed to the nearest 0.1 mg.

Boat surveys were conducted at each of the six sites to estimate boat traffic, as well as diving and snorkelling pressure. Each site was visited twice during peak hours (10 am—2 pm), giving a total of 8 h of surveys per site. Three types of boats were differentiated: boats that passed through the sampling area but did not stop, diving boats that stopped at the sites and dropped divers, and snorkelling boats that stopped at the sites and dropped snorkelers. Snorkelling boats were further differentiated between the traditional long-tail boats carrying a maximum of 5 snorkelers and "large boats" that could carry up to 50 passengers.

2.2. Data analysis

2.2.1. Coral community structure

The percent cover of hard corals was calculated for each 15 m transect by dividing the sum of all hard coral distances measured under each transect line by 1500 cm. We compared differences in hard coral cover between MPA and non-MPA sites, between past high-use and past low-use sites, and among sites in general using 1-way analyses of variance (ANOVA). Data were square-root transformed to meet assumptions of normality (Shapiro—Wilks test). Tukey's HSD tests were also run to determine the significance of dissimilarities among sites.

To compare the taxonomic composition of corals among sites, the three most abundant families (Acroporidae, Agariciidae, and Poritidae) were considered as separate taxonomic groups, and all other families were grouped into a category termed "Other". Two-factor ANOVAs were then used to compare the mean percent cover of these four taxonomic groups among sites, when sites were categorised by 1) MPA status (fixed factors: MPA status and coral family), and 2) past level of recreational use (fixed factors: usage level and coral family). Data were square-root transformed to meet assumptions of normality (Shapiro—Wilks test). Tukey's HSD tests were also run to determine the significance of dissimilarities among sites.

Data collected during the study period were also compared to a seven-year database maintained by the Save Koh Tao group (SKT). The database contains survey data collected from 2006 to 2012, prior to the establishment of MPAs, using 100 m long fixed transect lines and the "point-intercept survey" method to record coral cover and growth form diversity (% cover of branching, massive, submassive, foliose, encrusting colonies) at each of the six sites surveyed in the present study (see Save Koh Tao database at: www.marineconservationkohtao.com). One-factor ANOVAs were also performed on the SKT baseline data to compare the mean percent cover of foliose and branching growth forms between past high use and low use sites.

2.2.2. Coral health

Disease prevalence was calculated for each 30 m² belt transect by dividing the number of diseased colonies by the total number of colonies examined. We then compared disease prevalence: 1) between sites differing in MPA status, 2) between sites differing in past recreational use, and 3) among sites in general, using the non-parametric Kruskal—Wallis test (data did not meet assumptions of normality). Multiple post-hoc, pairwise comparisons were then performed using Dunn's procedure with Bonferroni corrections, to determine the significance of dissimilarities.

Calculations of the prevalence of other compromised health categories and statistical comparisons of these categories among sites were performed using the procedures described above for disease prevalence.

2.2.3. Environmental characteristics

Diving pressure at each site was calculated as the number of dive boats observed/hour. Eight hours of surveys were available for all sites but for Twins, which had only 4 h of reliable data because of extreme weather conditions on one of the surveys that prevented boat access to the site. Diving pressure was then compared between sites grouped according to MPA status and past use, and among sites in general using the non-parametric Kruskal—Wallis test.

Snorkelling pressure at each site was calculated as the number of snorkelling boats observed/hour. Big snorkelling boats were counted as equivalent to 10 small snorkelling boats. Analyses described above for diving pressure were repeated for snorkelling pressure.

Boat traffic at each site was calculated as the total number of boats (passing boat + snorkelling boat + diving boat) observed on site/hour. Analyses described above for diving pressure were repeated for boat traffic.

The weight of sediment in each trap was divided by the number of days the traps had been underwater to calculate sedimentation rate (gm sediment/day). Sedimentation rates were then compared: 1) between sites differing in protection status, 2) between sites differing in past use, and 3) among sites in general, using the non-parametric Kruskal—Wallis test.

2.2.4. Relationship between past use and coral health

A correlation matrix using Pearson's coefficient (5% significance level) was computed to identify trends in univariate relationships between past use and measures of coral community structure (i.e. percent coral cover, prevalence of the Acroporidae and Agaricidae) and measures of coral health (i.e. prevalence of disease and other indicators of compromised health). Univariate analyses were performed using Microsoft Excel (V14.3.8) and XLSTAT (203.5.03).

Resemblance matrices were created for measures of coral health (i.e., total prevalence of disease, algae overgrowth, Drupella scars, and coral breakage) and environmental variables (i.e. sedimentation rate, boat traffic, diving pressure, and snorkelling pressure) based on the Bray—Curtis index of similarity, which has been described as the most appropriate index for the description of benthic assemblages (Anderson, 2001). The biological data were square-root transformed due to strong linear relationships between some pairs of variables (Anderson et al., 2008). Environmental data were normalised (z-transformed, where average = 0 and standard deviation = 1).

Similarities between coral health assemblages were illustrated using a non-metric multidimensional scaling plot (MDS). A 2-factor crossed analysis of similarity (ANOSIM) was used to test differences in coral health assemblages between MPA status and past recreational use (Anderson et al. 2008). Multivariate analyses were performed in PRIMER v6 and PERMANOVA + add-in (PRIMER-E Ltd, Plymouth, UK).

3. Results

3.1. Hard coral cover

Mean percent hard coral cover was generally high across all sites (mean \pm SE: $62 \pm 8.3\%$; range: 43%–88%; Fig. 2), although it differed significantly among sites (F = 4.416, df = 5, p = 0.016; Fig. 2). Mean hard coral cover was twice as high at Hin Wong compared to Ao leuk (Fig. 2). Both are currently non-MPA sites, but Hin Wong (highest coral cover) is a past low-use site, whereas Ao leuk (lowest coral cover) is a past high-use site.

When sites were grouped according to MPA status, mean percent coral cover did not differ statistically between MPA vs non-MPA sites (F = 1.376, df = 1, p = 0.258). Similarly, mean percent cover did not differ statistically between sites grouped according to past high versus low recreational use (F = 2.464, df = 1, p = 0.136; Fig. 2). However, highest mean hard coral cover was recorded at a past low-use site and lowest cover (by more than two-fold) at a past high-use site; both of these sites are currently non-MPAs (Fig. 2).

3.2. Coral family assemblage

Percent cover of individual coral families did not differ statistically between sites differing in either current MPA status (F = 0.453, df = 1, p = 0.503) or past recreational use (F = 0.168, df = 1, p = 0.684; Fig. 3). Nevertheless, mean percent cover of the Acroporidae was more than two-fold greater in non-MPA compared to MPA sites, and also more than two-fold greater in past low-use compared to high-use sites (Fig. 3). Conversely, percent cover of the Agariciidae was almost two-fold greater in past high-use compared to low-use sites (Fig. 3), suggesting a possible inverse relationship between the percent cover of the Acroporidae and Agariciidae at sites when grouped according to past usage.

Furthermore, analysis of the 7-year baseline data from SKT revealed a significant inverse relationship in the abundance of corals with a foliose growth form (mostly Agariciidae) compared to those with a branching growth form (mostly Acroporidae) at the study sites. Percent cover of foliose corals was more than two-fold greater than the cover of branching corals at high-use sites, whereas the inverse was true at low-use sites (T-test: p < 0.02 and p < 0.001, respectively).

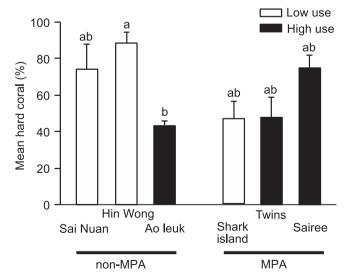


Fig. 2. Comparison of mean (\pm SE) hard coral cover among six study sites (3 MPA and 3 non-MPA sites) surveyed around the island of Koh Tao. Black histograms denote past high-use sites; white histograms denote past low-use sites. Letters above histograms represent significant groups using a Tukey's HSD post-hoc analysis (p < 0.05).

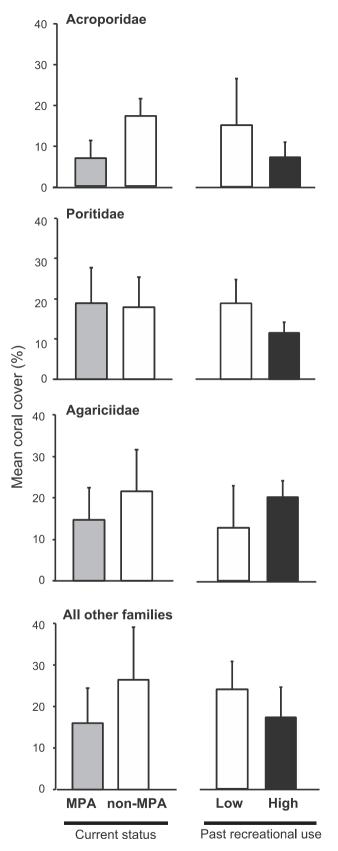


Fig. 3. Comparison of mean (\pm SE) hard coral cover for four categories of coral families between sites differing in current MPA status (MPA vs non-MPA, left pair of histograms) or past recreational use (high-use vs low-use, right pair of histograms). MPA sites comprise 2 past high-use sites and 1 past low-use site; non-MPA sites comprise 2 past low-use sites and 1 past high-use site. n=9 transects per current status or past use category.

3.3. Coral health

3.3.1. Disease prevalence

The health status of 6373 coral colonies was recorded across all six sites. Overall, mean disease prevalence was low $(0.72\% \pm 0.3\%)$, with only three types of disease recorded at all sites combined: white syndromes, growth anomalies and skeletal eroding band disease. Mean disease prevalence was 1.7 times higher inside compared to outside MPAs. However, disease prevalence did not differ statistically between sites differing in MPA status (Kruskal–Wallis: df = 1, p = 0.604; Fig. 4). Mean disease prevalence was higher (by 1.2-fold) at past high-use sites, although again, such differences were not statistically significant (Kruskal–Wallis: df = 1, P = 0.671; Fig. 4).

Growth anomalies were 20 times more prevalent at sites inside than outside current MPAs, and similarly more prevalent at past high-use compared to low-use sites (Fig. 4). The prevalence of white syndromes, however, was more than two-fold greater at current non-MPA sites and past low-use sites (Fig. 4). Prevalence of skeletal eroding band disease was very low and only present inside the MPA framework, at a past low-use site (Shark island) (Fig. 4).

3.3.2. Other compromised health indicators

Nine other indicators of compromised coral health were recorded: grazing scars, sediment damage, coral breakage, crown-of-thorns starfish predation, *Drupella* snail predation, sponge overgrowth, algal overgrowth, environmentally induced bleaching (non-focal bleaching), and pigmentation response. Although overall, mean values for the prevalence of other indicators of compromised health were 2-fold higher inside compared to outside current MPAs, and also almost 2-fold higher at past high-use compared to low-use sites, these differences were not statistically significant for either MPA status (Kruskal—Wallis, df = 1, p = 0.660; Fig. 5) or past recreational use (Kruskal—Wallis, df = 1, p = 0.379; Fig. 5).

Of the other indicators of compromised health recorded, predation by *Drupella* snails, algae overgrowth, sediment damage, and breakage were the most prevalent. All categories but sediment damage and environmentally-induced bleaching were also most prevalent in current MPAs and past high-use sites (Fig. 5).

The non-metric multidimensional scaling plot representing coral health assemblages showed slight clustering among sites by status, with MPA sites (white symbols) tending to be distributed lower on the plot than non-MPA sites (black symbols) (Fig. 6). However, statistically, distributions of coral health assemblages did not differ significantly between sites differing in MPA status, although the p value indicates that any similarities were marginal (ANOSIM: Global R = 0.481, p = 0.05; Fig. 6).

While no clustering of sites was apparent on the MDS plot in terms of past recreational use, statistically, the distributions of coral health assemblages differed significantly between use levels (ANOSIM: Global R=0.556, p=0.001; Fig. 6). Algae overgrowth, *Drupella* predation, and breakage appeared to strongly affect both non-MPA/low-use sites (black diamonds) and MPA/high-use sites (white circles) (Fig. 6). Disease prevalence provided the greatest explanatory power for coral health assemblages at the MPA low-use site (white diamonds) (Fig. 6).

3.4. Environmental and local pressures

3.4.1. MPA status comparison

Sedimentation rates were significantly greater at current MPA sites compared to non-MPA sites (Kruskal-Wallis: df = 1, p = 0.043). Mean non-anchoring boat traffic was also greater at MPA sites, but differences were not statistically significant (Kruskal-Wallis: df = 1, p = 0.577). Diving pressure did not differ

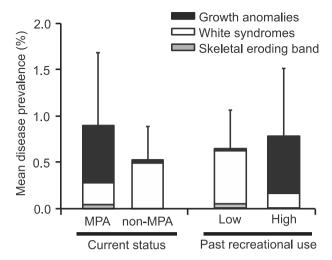


Fig. 4. Comparison of mean coral disease prevalence (\pm SE) for each of three coral diseases recorded at sites around the island of Koh Tao differing in current MPA status (left) and past recreational use (right).

between sites differing in MPA status, being equally high at MPA and non-MPA sites (Kruskal-Wallis: df = 1, p = 0.306). In contrast, snorkelling pressure was absent at MPA sites (Kruskal-Wallis: df = 1, p = 0.001).

3.4.2. Recreational use comparison

Statistically, none of the 4 indicators of environmental or anthropogenic pressure differed between past recreational use categories. However, mean sedimentation rates were more than three-fold greater at past high-use sites compared to low-use sites (High use: Mean = 0.1 ± 0.03 ; Low use: Mean = 0.03 ± 0.004 ; Kruskal—Wallis: df = 1, p = 0.270). Boat traffic was nearly two-fold greater at high-use sites (High-use: Mean = 15.2 ± 3.6 ; Low-use: Mean = 8.3 ± 1.1 ; Kruskal—Wallis: df = 1, p = 0.731). Mean diving pressure was two-fold higher at high-use sites (High-use: Mean = 1.9 ± 0.5 ; Low-use: Mean = 0.9 ± 0.2 ; Kruskal—Wallis: df = 1, p = 0.297), although mean snorkelling pressure was higher at low-use sites (High-use: Mean = 1.25 ± 0.4 ; Low-use: Mean = 2.7 ± 0.8 ; Kruskal—Wallis: df = 1, p = 0.240).

3.5. Relationship between recreational use and coral health

Boat traffic was positively correlated with sedimentation rate, algal overgrowth, and *Drupella* prevalence (Fig. 7). Algal

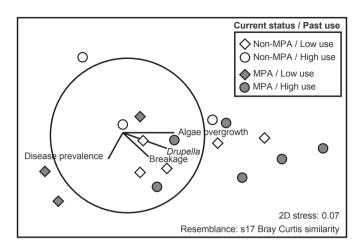
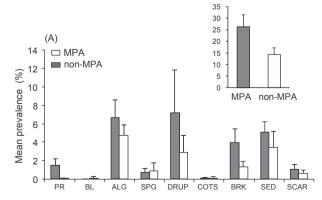


Fig. 6. Non-metric multidimensional scaling analysis (nMDS) plot with vectors (Pearson's correlation) representing variables (prevalence of disease or other indicators of compromised coral health) driving similarities (Bray—Curtis matrix) in coral health assemblages among sites. Symbols and colours represent the combined MPA status and recreational use category for each transect. n=3 transects per site.

overgrowth and *Drupella* prevalence were also both positively correlated with prevalence of the foliose family Agariciidae, while sedimentation was negatively correlated with prevalence of the branching family Acroporidae (Fig. 7). There is thus a possible feedback loop, in which increased boat traffic and sedimentation decrease cover of branching corals in the family Acroporidae, providing space for weedy corals in the family Agariciidae to colonise, particularly as *Drupella* predation and algal overgrowth are positively correlated with the abundance of this latter family. Such a loop would lead to an overall decrease in coral diversity and health. Coral breakage was also negatively correlated with hard coral cover (Fig. 7).

4. Discussion

Coral health surveys at sites within three newly established MPAs and three control (non-MPA) sites, one year after the new protection framework had been established, revealed that coral health and community structure around Koh Tao were more reflective of past recreational use than current MPA protection status. At sites inside the MPA framework, means for all variables



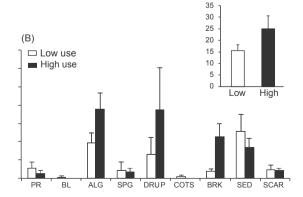


Fig. 5. Comparison of mean prevalence (±SE) among 9 indicators of compromised health between sites differing in (A) current MPA status, and (B) past recreational use. Inset graphs in each panel represent mean prevalence (±SE) for the sum of all indicators of compromised health. PR = pigmentation responses, BL = environmentally-induced bleaching, ALG = green algae overgrowth, SPG = sponge overgrowth, DRUP = Drupella scars, COTS = crown-of-thorns starfish scars, BRK = breakage, SED = tissue necrosis from sediment, SCAR = other grazing scars.

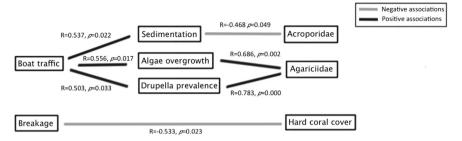


Fig. 7. Sketch representing the network of significant correlations (Pearson's) among biological and environmental factors affecting the two most abundant coral families (Acroporidae and Agariciidae) on Koh Tao reefs. Grey lines represent negative correlations; Black lines represent positive correlations.

studied (hard coral cover, structure of coral family assemblages, disease prevalence, and densities of colonies showing other signs of compromised health) followed patterns observed at past high-use sites (a status shared by 2 of the 3 MPA sites). Conversely, means for all variables studied at sites outside the MPA framework followed patterns found at past low-use sites (a status shared by 2 of the 3 non-MPA sites). Our study suggests that timeframes greater than one year following rezoning will be required to produce a potentially positive change in the health and diversity of coral communities of Koh Tao. A recent global analysis suggests that the capacity of MPAs to prevent coral loss is dependent on the duration of protection, with up to 15 years needed to effect positive changes inside MPAs in the Indo-Pacific (Selig and Bruno, 2010). The long timescale predicted reflects life history and community structure characteristics typical of Indo-Pacific coral reef communities, such as high disease susceptibility of the typically dominant coral family Acroporidae, and potential compliance issues for newly established MPAs. In our study, lack of information about fishing pressure around the island and about whether patterns have changed since the establishment of the MPAs raises questions about compliance with the new MPA zoning. However, because the rezoning is an initiative of the Koh Tao community and examples of good conduct have been documented, it is reasonable to assume that our estimation of the more than one year timeframe for the new MPA framework to effect a change is not confounded by compliance issues. At the very least, our study provides an important baseline for future evaluation of the capacity of these MPAs to ameliorate coral health.

4.1. Current state of Koh Tao's reef

Our study revealed overall high levels of mean hard coral cover and low levels of coral disease prevalence around the island of Koh Tao. Disease prevalence ranged from 0.1 to 1.8%, which is typical of the range recorded for reefs in parts of the Indo-Pacific (e.g. Great Barrier Reef, Northwest Hawaiian Islands; Ruiz-Morenol et al., 2012). Constant warm temperatures throughout the year preceding our surveys, coupled with an absence of thermal extremes (CS, unpubl. data), could have contributed to the overall low disease prevalence recorded during our surveys. Links between temperature anomalies and outbreaks of coral diseases are complex. For example, warm winters can increase coral host resistance to disease (e.g, production of antibiotics in coral mucus) (Ritchie, 2006; Heron et al., 2010), although mild winters can also maintain pathogen populations so that, if followed by hot summer anomalies, disease outbreaks can be triggered (Heron et al., 2010). We hypothesise that constant warm temperatures and the absence of acute temperature stress throughout the year preceding our surveys might explain the overall low disease prevalence we found on Koh Tao reefs. Levels of disease prevalence recorded in our study were also notably lower than the 30% prevalence levels reported by Lamb et al. (2014) for high-use sites on surveys two years prior to ours. However, their surveys were carried out a year after a mass bleaching event that is likely to have reduced the disease resistance of corals. Also, more reefs were surveyed in their study, notably the site "Japanese Gardens", which is one of Koh Tao's most visited dive sites, especially by novice divers.

Lower (by 1.7-fold) mean levels of disease at past low-use/ current non-MPA sites, where coral cover tended to be higher, is at odds with a number of studies that have found increased coral disease prevalence to be associated with high host abundance (Bruno et al., 2007; Myers and Raymundo, 2009; Ruiz-Moreno et al., 2012). High coral cover reduces the distance between neighbouring corals, thereby increasing the potential for transmission of pathogens and for competitive interactions among corals, which can create injuries that may become entry points for pathogens (Lang and Chornesky, 1990; Bruno et al., 2007; Chadwick and Morrow, 2011). It has also been hypothesised that high coral cover is associated with higher densities of corallivorous fish and invertebrates that are potential vectors of coral diseases (Bruno et al., 2007; Raymundo et al., 2009; Chong-Seng et al., 2011; Onton et al., 2011). In particular, the crown-of-thorns starfish Acanthaster planci and Drupella snails, both of which cause significant feeding injuries that facilitate infection, have been shown to be disease vectors (Antonius and Riegl, 1998; Bruno et al., 2007; Nugues and Bak, 2009; Onton et al., 2011; Nicolet et al., 2013; Katz et al., 2014). The high overall hard coral cover around the Island may thus constitute an increased risk for future disease outbreaks, particularly if an extreme environmental event, such as a warm thermal anomaly, reduces the disease resistance of local coral populations.

Evidence is emerging that hard coral cover is a poor indicator of reef condition (Edinger and Risk, 2000; Cleary et al., 2008; Darling et al., 2013). Sites with high coral cover may be composed of monospecific assemblages, and thus have low habitat complexity and low overall biodiversity (Aronson and Precht, 1995; Edinger and Risk, 2000). Interestingly, mean percent cover of the typically more disease- and disturbance-susceptible branching acroporids (e.g., Marshall and Baird, 2000; Willis et al., 2004; Wooldridge, 2014) was low at Koh Tao sites overall, but was more than twofold higher at past low-use sites (currently non-MPA sites). Conversely, corals in the typically weedy family Agariciidae, mostly represented by Pavona cactus, were almost two-fold more abundant at past high-use sites. These results are in line with a recent study, which found that reefs subjected to stress tended towards dominance by weedy species (Darling et al., 2013). Pavona species were thus characterised as "survivors", whereas Acropora species, which are vulnerable to multiple stressors, were characterised as "losers" (Darling et al., 2013). Branching corals are also believed to be the most vulnerable to diving impacts (Hasler and Ott 2008,

Guzner et al., 2010). With the current levels of environmental and anthropogenic pressures around Koh Tao, we predict that there is a risk of a gradual shift towards higher prevalence of mono-specific stands of Agariciidae around the Island (Rouphael and Inglis, 2002; Guzner et al., 2010).

4.2. Environmental and anthropogenic pressures and links to coral health

Diving pressure was extremely high, approximately 1.8 dive boats/hour, at sites currently classified as both MPAs and non-MPAs. Even using a low estimate of 20 divers/dive boat, this equates to at least 36 divers/hour, with a mean of around 150 divers per day at all 6 sites surveyed. The recommended carrying capacity for diving on coral reefs is 6000 divers per year (Hawkins and Roberts, 1997; Zakai and Chadwick-Furman, 2002), a limit that would be reached within 40 days at our study sites. The impact of recreational diving is of increasing concern for coral reefs (Davis and Tisdell, 1995; Barker and Roberts, 2004; Krieger and Chadwick, 2013). Divers directly affect corals through physical contact caused by touching, fin damage, and dangling equipment, and through sediment re-suspension caused by fins. Heavily dived sites have been associated with low cover of hard corals, of which a higher proportion of colonies are injured or diseased compared to sites with low diving activity (Hasler and Ott, 2008; Krieger and Chadwick, 2013; Lamb et al., 2014). Diving also has strong indirect effects on the reef. For example, increased predation by Drupella snails has been reported at heavily dived sites in Eliat. Israel (Guzner et al., 2010). In our study, predation by Drupella snails was linked with sedimentation and breakage associated with high boat traffic rather than high diving pressure per se. Drupella predation has been shown to decrease skeletal growth (Guzner et al., 2010), and to be associated with the transmission of brown band disease (Nicolet et al., 2013) and a range of other diseases, including white syndromes, black band disease and skeletal eroding band (Antonius and Riegl, 1998; Shafir et al., 2008; Onton et al., 2011). High levels of Drupella predation have been documented on Koh Tao reefs, with densities reaching up to 90 individuals on a single colony after the bleaching event in 2010 (Hoeksema et al., 2013). Our results suggest that Drupella preferentially attack corals experiencing physiological stress, a finding corroborated by Guzner et al. (2010), who also found higher abundance of Drupella on corals suffering physiological stress at heavily dive sites.

High levels of boat traffic were also associated with high algal overgrowth. Decreases in coral cover worldwide are leading to community phase shifts, with corals being replaced by macro-algal assemblages (McCook et al., 2001; Hughes et al., 2007). Algae typically proliferate after disturbances causing coral mortality, and once established, they reduce space available for coral recruits and juveniles (reviewed in Birrell et al., 2008; Barott et al., 2012). Some species of macro-algae also inhibit recruitment of coral larvae and/ or lead to increased mortality of coral recruits (Kuffner et al., 2006). Contact between algae and adult coral colonies can be deleterious to coral heath (Nugues, 2004; Thurber et al., 2012) and facilitate the spread of coral diseases (Smith et al., 2006), particularly if algae cause abrasions that serve as entry points for pathogens (McCook et al., 2001). More generally, algae have been shown to affect the fecundity, growth and survival of adult colonies, and alter the microbial symbiont communities of corals (Hughes et al., 2007; Thurber et al., 2012). Increases in nutrients, pollution, and sea temperatures, and decreases in herbivory have all been suggested as potential factors that increase algal overgrowth on reefs (Aronson and Precht, 2001; Szmant, 2002; Nugues et al., 2004). The increases in algal overgrowth associated with increased sedimentation in our study is in line with a recent study in which increased sedimentation increased the growth of turf algae, probably due to increased availability of nutrients from the sediments (Goatley and Bellwood, 2013). Moreover, sedimentation alone can affect the health of corals, increasing the potential for contact with pathogens and contaminants, physically abrading coral tissues, decreasing energy available through sediment shading, and increasing energetic costs associated with sediment removal and impaired feeding (Fabricius, 2005; Haapkyla et al., 2011; Erftemeijer et al., 2012). Pollock et al. (2014) also found a high correlation between sediment tissue necrosis and the prevalence of white syndromes, further highlighting the implications of sediment stress on the long-term health of corals around the Island.

The high levels of diving pressure, boat traffic and sedimentation remaining on reefs inside recently established MPAs surrounding the island of Koh Tao raises questions about the capacity of the protected areas to ameliorate coral health. MPAs have been advocated as a strong tool to mitigate phase-shifts from coral to algal-dominated reefs (Hughes et al., 2007). When user compliance is high, MPAs have the potential to maintain or increase herbivory, which then controls macro-algal abundance and has the potential to increase the resilience of coral communities (Hughes et al., 2007). However, the question remains whether potential increased herbivory at these highly disturbed reefs will be enough to mitigate algal overgrowth. Further studies are needed to fully characterise the status of herbivory inside and outside these MPAs.

5. Conclusions

This study represents a strong baseline for future studies of the capacity of MPAs to protect and possibly enhance coral health and diversity around the island of Koh Tao. So far, health and diversity of the local coral communities reflect the history of past recreational use, with past high-use sites characterised by lower hard coral cover, lower prevalence of the disease- and disturbance-susceptible coral family Acroporidae, and conversely, higher prevalence of the weedy family Agariciidae. Generally higher mean levels of coral disease and other indicators of compromised health at past highuse sites are likely to be at least partially caused by higher sedimentation, boat traffic and diving pressure at these sites than at past low-use sites. One challenge for the successful management of the reefs of Koh Tao is that the recently established MPA framework mostly encompasses past high-use sites. Our study reveals that past high-use sites now inside MPAs were the most strongly affected by sedimentation and displayed highest levels of algal overgrowth, predation by Drupella, and breakage. Moreover, with the current rate of tourism development, past low-use sites are quickly becoming high-use sites. The creation of MPAs that only address the issue of fishing pressure, with no further incentives to control tourism expansion, is thus likely to be insufficient to protect the Island's coral reefs. Other measures, such as seasonal closures of some sites, and/or limits to the number of divers allowed at each site per year should be considered. However, the large number of threats and degraded reef condition found in this study makes the reefs of Koh Tao a useful study area for future long-term evaluation of the role of MPAs in ameliorating the health of coral communities.

Acknowledgements

This project was funded by the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies and James Cook University. We thank Devrim Zahir, Fanny Couture and the team from the New Heaven Reef Conservation Program in Koh Tao for their assistance in the field, and Dr Wayne Phillips and Mahidol University in Bangkok for assistance with the sediment samples.

We also thank Dr JB Raina for his constructive comments on this manuscript.

References

- Aeby, G.S., Williams, G.J., Franklin, E.C., Haapkyla, J., Harvell, C.D., et al., 2011. Growth anomalies on the coral genera Acropora and Porites are strongly associated with host density and human population size across the Indo-Pacific. PLoS ONE 6 (2), e16887. http://dx.doi.org/10.1371/journal.pone.0016887.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26 (1), 32–46.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
- Antonius, A., Riegl, B., 1998. Coral diseases and *Drupella cornus* invasion in the Red Sea. Coral Reefs 17, 48.
- Aronson, R.B., Precht, W.F., 1995. Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. J. Exp. Mar. Biol. Ecol. 192, 1–14.
- Aronson, R.B., Pretch, W.F., 2001. Evolutionary paleoecology of Caribbean coral reefs. In: Allmon, D., Bottjer, D.J. (Eds.), Evolutionary Paleoecology: the Ecological Context of Macroevolutionary Change. Columbia University Press, New York, NY, pp. 171–233.
- Barott, K.L., Williams, G.J., Vermeij, M.J., Harris, J., Smith, J.E., Rohwer, F.L., Sandin, S.A., 2012. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. Mar. Ecol. Prog. Ser. 460, 1–12.
- Barker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biol. Conserv. 120, 481–489.
- Beeden, R., Willis, B.L., Raymundo, L.J., Page, C.A., Weil, E., 2008. Underwater Cards for Assessing Coral Health on Indo-Pacific Reefs. Coral Reef Targeted Research and Capacity Building for Management Program. Currie Communications, Melbourne, p. 22. http://gefcoral.org/Portals/53/downloads/disease_products/0807%20Indo%20Pacific%20Underwater%20ID%20Cards.pdf.
- Birrell, C.L., McCook, L.J., Willis, B.L., Diaz-Pulido, G.A., 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. In: Gison, R.N., Atkinson, R.J.A., Gordon, J.D.M. (Eds.), Oceanography and Marine Biology: an Annual Review, vol. 46, pp. 25–63.
- Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., et al., 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. PLoS Biol. 5, 1220–1227. http://dx.doi.org/10.1371/journal.pbio.0050124.
- Burke, L., Reitar, K., Spalding, M., Perry, K., 2012. Reefs at Risk Revisited in the Coral Triangle. World Resource Institute, ISBN 978-1-56973-791-0.
- Chadwick, N.E., Morrow, K.M., 2011. Competition among sessile organisms on coral reefs. In: Coral Reefs: an Ecosystem in Transition. Springer, Netherlands, pp. 347–371.
- Chavanich, S., Viyakarn, V., Adams, P., Klammer, J., Cook, B., 2012. Reef communities after the 2010 mass coral bleaching at Racha Yai Island in the Andaman Sea and Koh Tao in the Gulf of Thailand. Phuket Mar. Biol. Cent. Res. Bull. 71, 103—110.
- Chong-Seng, K.M., Cole, A.J., Pratchett, M.S., Willis, B.L., 2011. Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease. Coral Reefs 30, 473–481.
- Cleary, D.F., De Vantier, L., Vail, L., Manto, P., de Voogd, N.J., Rachello-Dolmen, P.G., et al., 2008. Relating variation in species composition to environmental variables: a multi-taxon study in an Indonesian coral reef complex. Aquat. Sci. 70 (4), 419–431.
- Coelho, V.R., Manfrino, C., 2007. Coral community decline at a remote Caribbean island: marine no-take reserves are not enough. Aquat. Conserv. Mar. Freshw. Ecosyst. 17. 666–685.
- Danovaro, R., Bongiorni, L., Corinaldesi, C., Giovannelli, D., Damiani, E., Astolfi, P., Greci, L., Pusceddu, A., 2008. Sunscreens cause coral bleaching by promoting viral infections. Environ. Health Perspect. 116, 441–447.
- Darling, E.S., McClanahan, T.R., Côté, I.M., 2013. Life histories predict coral community disassembly under multiple stressors. Glob. Change Biol. 19, 1930–1940.
- Davis, D., Tisdell, C., 1995. Recreational scuba-diving and carrying capacity in marine protected areas. Ocean Coast. Manag. 26, 19–40.
- De'ath, G., Fabricius, K.E., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol. Appl. 10, 840–850.
- De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc. Natl. Acad. Sci. U. S. A. 109 (44), 17995–17999.
- Degnbol, P., Gislason, H., Hannac, S., Jentoftd, S., Nielsena, J.R., Sverdrup-Jensena, S., Wilsona, D.C., 2006. Painting the floor with a hammer: technical fixes in fisheries management. Mar. Policy 30, 534–543.
- Edinger, E.N., Risk, M.J., 2000. Reef classification by coral morphology predicts coral reef conservation value. Biol. Conserv. 92, 1–13.
- Erftemeijer, P.L., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. Mar. Pollut. Bull. 64 (9), 1737–1765.
- Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146. http://dx.doi.org/ 10.1016/J.MARPOLBUL.2004.11.028.
- Gardner, W.D., 1980. Field assessment of sediment traps. J. Mar. Res. 38, 41-45.
- Goatley, C.H.R., Bellwood, D.R., 2013. Ecological consequences of sediment on highenergy coral reefs. PloS ONE 8 (10), e77737. http://dx.doi.org/10.1371/ journal.pone.0077737.

- Graham, N.A., Ainsworth, T.D., Baird, A.H., Ban, N.C., Bay, L.K., Cinner, J.E., et al., 2011. From microbes to people: tractable benefits of no-take areas for coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 49, 105.
- Guzner, B., Novplansky, A., Chadwick, N.E., 2010. Indirect impacts of recreational scuba diving: patterns of growth and predation in branching stony corals. Bull. Mar. Sci. 86, 727–742.
- Haapkyla, J., Unsworth, R.K.F., Flavell, M., Bourne, D.G., Schaffelke, B., Willis, B.L., 2011. Seasonal rainfall and runoff promote coral disease on an inshore reef. PLoS ONE 6 (2), e16893.
- Halpern, B.S., Warner, R.R., 2003. Matching marine reserve design to reserve objectives. Proc. R. Soc. Lond. Ser. B 270, 1871–1878.
- Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., et al., 1999. Emerging marine diseases-climate links and anthropogenic factors. Science 285 (5433), 1505–1510.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., et al., 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296, 2158–2162
- Harvell, C.D., Jordán-Dahlgren, E., Merkel, S., Rosenberg, E., Raymundo, L., Smith, G., et al., 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. Oceanography 20, 172–195.
- Harvell, D., Altizer, S., Cattadori, I.M., Harrington, L., Weil, E., 2009. Climate change and wildlife diseases: when does the host matter the most? Ecology 90 (4), 912–920.
- Hasler, H., Ott, J.A., 2008. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea. Mar. Pollut. Bull. 56, 1788–1794.
- Hawkins, J.P., Roberts, C.M., 1997. Estimating the carrying capacity of coral reefs for scuba diving. In: Proceedings of the 8th International Coral Reef Symposium, vol. 2, pp. 1923–1926.
- Heron, S.F., Willis, B.L., Skirving, W.J., Eakin, C.M., Page, C.A., Miller, I.R., 2010. Summer hot snaps and winter conditions: modelling white syndrome outbreaks on Great Barrier Reef corals. PLoS ONE 5 (8), e12210.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2008. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742.
- Hoeksema, B.W., Scott, C., True, J.D., 2013. Dietary shift in corallivorous Drupella snails following a major bleaching event at Koh Tao, Gulf of Thailand. Coral Reefs 32 (2), 423–428.
- Hughes, T.P., Rodriguez, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B.L., 2007. Phase shifts, herbivory and resilence of coral reefs to climate change. Curr. Biol. 17, 360–365. http://dx.doi.org/10.1016/j.cub.2006.12.049.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., JBourque, J.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.
- Jameson, S.C., Tupper, M.H., Ridley, J.M., 2002. The three screen doors: *can* marine 'protected' areas be effective? Mar. Pollut. Bull. 44, 1177—1183.
- Kaczmarsky, L.T., 2006. Coral disease dynamics in the central Philippines. Dis. Aquat. Org. 69 (1), 9–21.
- Katz, S., Pollock, F.J., Bourne, D.G., Willis, B.L., 2014. Crown of Throns seastar predation and physical injury promote Brown band Disease on corals. Coral reefs 1–12.
- Krieger, J.R., Chadwick, N.E., 2013. Recreational diving impacts and the use of predive briefings as a management strategy on Florida coral reefs. J. Coast. Conserv. 17 (1), 179–189.
- Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R., Beach, K.S., 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar. Ecol. Prog. Ser. 323, 107–117.
- Lamb, J.B., Willis, B.L., 2011. Using coral disease prevalence to assess the effects of concentrating tourism activities on offshore reefs in a tropical marine park. Conserv. Biol. 25, 1044–1052.
- Lamb, J.B., True, J.D., Piromvaragorn, S., Willis, B.L., 2014. Scuba diving damage and tourist intensity of tourist activities increases coral disease prevalence. Biol. Conserv. http://dx.doi.org/10.1016/j.biocon.2014.06.027 (in press).
- Lang, J.C., Chornesky, E.A., 1990. Competition between scleractinian reef corals—a review of mechanisms and effects. In: Dubinsky, Z. (Ed.), Ecosystems of the World, Coral Reefs, vol. 25. Elsevier, Amsterdam, pp. 209—252.
- Marshall, P.A., Baird, A.H., 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19 (2), 155–163.
- Maynard, J.A., Anthony, K.R.N., Harvell, C.D., Burgman, M.A., Beeden, R., Sweatman, H., Heron, S.F., Lamb, J.B., Willis, B.L., 2011. Predicting outbreaks of a climate-driven coral disease in the Great Barrier Reef. Coral Reefs 30, 485–495.
- McClanahan, T.R., 2008. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia 155, 169—177.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19 (4), 400–417.
- Myers, R.L., Raymundo, L.J., 2009. Coral disease in Micronesian reefs: a link between disease prevalence and host abundance. Dis. Aquat. Org. 87 (1–2), 97–104.
- Nichols, R.S., 2013. Effectiveness of Artificial Reefs as Alternative Dive Sites to Reduce Diving Pressure on Natural Coral Reefs, a Case Study of Koh Tao, Thailand (Doctoral dissertation). University of Cumbria.

- Nicolet, K.J., Hoogenboom, M.O., Gardiner, N.M., Pratchett, M.S., Willis, B.L., 2013. The corallivorous invertebrate Drupella aids in transmission of brown band disease on the Great Barrier Reef. Coral Reefs 32 (2), 585–595.
- Nugues, M.M., Smith, G.W., Hooidonk, R.J., Seabra, M.I., Bak, R.P.M., 2004. Algal contact as a trigger for coral disease. Ecol. Lett. 7, 919–923.
- Nugues, M.M., Bak, R.P.M., 2009. Brown-band syndrome on feeding scars of the crown-of-thorn starfish *Acanthaster planci*. Coral Reefs 28, 507–510.
- Onton, K., Page, C.A., Wilson, S.K., Neale, S., Armstrong, S., 2011. Distribution and drivers of coral disease at Ningaloo reef, Indian Ocean. Mar. Ecol. Prog. Ser. 433, 75–84
- Page, C.A., Baker, D.M., Harvell, C.D., Golbuu, Y., Raymundo, L., Neale, S.J., Rosell, K.B., Rypien, K.L., Andras, J.P., Willis, B.L., 2009. Influence of marine reserves on coral disease prevalence. Dis. Aquat. Org. 87, 135—150.
- Platong, S., Chaloem, S., Charoenmart, K., et al., 2012. Strategic Plan: Integrated Coastal Management for Koh Tao. Center for Biodiversity of Peninsular Thailand. Prince of Songkla University. Hat Yai. Thailand.
- Pollock, F.J., Lamb, J.B., Field, S.N., Heron, S.F., Schaffelke, B., Shedrawi, G., et al., 2014. Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. PloS ONE 9 (7), e102498.
- Raymundo, L.J., Halford, A.R., Maypa, A.P., Kerr, A.M., Karl, D.M., 2009. Functionally diverse reef- fish communities ameliorates coral disease. PNAS 106 (40), 17067–17070.
- Richardson, L.L., 1998. Coral diseases: what is really known? Trends Ecol. Evol. 13 (11), 438–443.
- Ritchie, K.B., 2006. Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Mar. Ecol. Prog. Ser. 322, 1–14.
- Roder, C., Arif, C., Bayer, T., Aranda, M., Daniels, C., Shibl, A., et al., 2013. Bacterial profiling of white plague disease in a comparative coral species framework. ISME J..
- Rouphael, A.B., Inglis, G.J., 2002. Increased spatial and temporal variability in coral damage caused by recreational scuba diving. Ecol. Appl. 12, 427–440.
- Ruiz-Morenol, D., Willis, B.L., Page, C.A., Weil, E., Cróquer, A., Vargas-Angel, B., et al., 2012. Global coral disease prevalence associated with sea temperature anomalies and local factors. Dis. Aquat. Org. 100, 249–261.
- Sato, Y., Bourne, D.G., Willis, B.L., 2009. Dynamics of seasonal outbreaks of black band disease in an assemblage of Montipora species at Pelorus Island (Great Barrier Reef, Australia). Proc. R. Soc. Lond. B Biol. Sci. 276, 2795–2803.
- Scott, C., 2012. Koh Tao Biorock: Artificial Reef and Alternative Dive Site. Project proposal. Chad Scott, Marine Project Coordinator, Save Koh Tao Marine Branch, Koh Tao, Thailand.
- Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5 (2), e9278. http://dx.doi.org/10.1371/journal.pone.0009278.
- Sethapun, T., 2000. Marine National Park in Thailand.
- Shafir, S., Gur, O., Rinkevich, B., 2008. A *Drupella cornus* outbreak in the northern Gulf of Eilat and changes in coral prey. Coral Reefs 27, 379.
- Sutherland, K.P., Ritchie, K.B., 2004. White pox disease of the Caribbean elkhorn coral, Acropora palmata. In: Coral Health and Disease. Springer, Berlin Heidelberg, pp. 289–300.

- Szmant, A.M., 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25, 743–766.
- Smith, J.E., Shaw, M., Edwards, R.A., Obura, D., Pantos, O., et al., 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. Ecol. Lett. 9, 835–845
- Szuster, B.W., Dietrich, J., 2014. Small island tourism development plan implementation: The Case of Koh Tao, Thailand, Enviro, Asia 7 (2), 124–132.
- Thurber, R.V., Burkepile, D.E., Correa, A.M., Thurber, A.R., Shantz, A.A., Welsh, R., et al., 2012. Macroalgae decrease growth and alter microbial community structure of the reef-building coral, Porites astreoides. PloS ONE 7 (9), e44246.
- Van der Meij, S.E., Hoeksema, B.W., 2010. Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920—2005). Mar. Pollut. Bull. 60 (9), 1442—1454.
- Vargas-Angel, B., 2009. Coral health and disease assessment in the U.S. Pacific remote island areas. Bull. Mar. Sci. 84, 211–227.
- Weil, E., Irikawa, A., Casareto, B., Suzuki, Y., 2012. Extended geographic distribution of several Indo-Pacific coral reef diseases. Dis. Aquat. Org. 98 (2), 163–170.
- Weterings, R., 2011. A GIS-based assessment of threats to the natural environment on Koh Tao, Thailand. Kasetsart J. Nat. Sci. 755, 743–755.
- Wilkinson, C., Brodie, J., 2011. Catchment Management and Coral Reef Conservation: a Practical Guide for Coastal Resource Managers to Reduce Damage from Catchment Areas Based on Best Practice Case Studies. Global Coral Reef Monitoring Network, p. 120.
- Williams, G.J., Knapp, I.S., Work, T.M., Conklin, E.J., 2011a. Outbreak of *Acropora* white syndrome following a mild bleaching event at Palmyra Atoll, Northern Line Islands, Central Pacific. Coral Reefs 30 (3), 621.
- Williams, G.J., Knapp, I.S., Aeby, G.S., Davy, S.K., 2011b. Spatial and temporal patterns of scleractinian coral, soft coral, and zoanthid disease on a remote, near-pristine coral reef (Palmyra Atoll, central Pacific). Dis. Aquat. Org. 94 (2), 89–100.
- Williams, G.J., Price, N.N., Ushijima, B., Aeby, G.S., Callahan, S., Davy, S.K., et al., 2014. Ocean warming and acidification have complex interactive effects on the dynamics of a marine fungal disease. Proc. R. Soc. B Biol. Sci. 281 (1778), 2013—3069.
- Willis, B.L., Page, C.S., Dinsdale, E.A., 2004. Coral disease on the Great Barrier Reef. In: Rosenberg, E., Loya, Y. (Eds.), Coral Disease and Health. Springer, Berlin, pp. 69–104.
- Wooldridge, S.A., 2014. Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host. Coral Reefs 33 (1), 15–27.
- Wongthong, P., Harvey, N., 2014. Integrated coastal management and sustainable tourism: a case study of the reef-based SCUBA dive industry from Thailand. Ocean Coast. Manag. 95, 138–146.
- Yeemin, T., Sutthacheep, M., Pettongma, R., 2006. Coral reef restoration projects in Thailand. Ocean Coast. Manag. 49 (9), 562–575.
- Zakai, D., Chadwick-Furman, N.E., 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biol. Conserv. 105 (2), 179–187.